HELSINGIN YLIOPISTO
HELSINGFORS UNIVERSITET
UNIVERSITY OF HELSINKI

Changes in lake diatom assemblages in Northwestern Finnish Lapland over recent decades and their relation to climate warming

Master's programme in
Environmental Change and
Global Sustainability
Master's thesis
May 2021

Maxime Courroux
Supervisors:
Kaarina Weckström
Jan Weckström
Maija Heikkilä

Tiedekunta - Fakultet - Faculty

Faculty of Biological and Environmental Sciences

Tekijä - Författare - Author

Maxime Courroux

Työn nimi - Arbetets titel - Title

Changes in lake diatom assemblages in Northwestern Finnish Lapland over recent decades and their relation to climate warming

Oppiaine - Läroämne - Subject

Environmental Change and Global Sustainability

Työn laji/ Ohjaaja - Arbetets art/Handledare - Level/Instructor:	Aika - Datum - Month and year	Sivumäärä - Sidoantal - Number of pages
Master's Thesis Master's Thesis / Supervisor's Name Kaarina Weckström, Jan Weckström, Maija Heikkilä	May 2021	35 pp. + 9 pp. appendices

Tiivistelmä - Referat - Abstract

The changes in lake diatom assemblages as a response to climate warming over the past three decades were examined in 26 lakes across Northwestern Finnish Lapland using multivariate statistical techniques. The lakes are distributed along a steep climatic and vegetational gradient, covering three distinct vegetation zones spanning boreal coniferous forest, mountain birch woodland, and treeless tundra. Lakes were selected following a study realised by Weckström and Korhola in 2001, who had sampled the same lakes for surface-sediment diatom assemblages, physical, and chemical limnological variables. Climate data from the past 30 years was retrieved, showing a slow and steady yearly increase in temperature, with strong seasonal fluctuation and fall months experiencing the strongest warming. Surface sediment samples were taken from the lakes and their diatom communities analysed. A total of 185 diatom taxa representing 27 genera were recorded. Ordination techniques (DCA, CCA) at the genus and species level were performed to identify the main patterns of variation between diatom data from the original data set and the current study, and their relationship to environmental variables. Strong changes were recorded in four of the lakes with major shifts in dominant diatom species. Moderate changes were recorded in eight lakes, where dominance changes were recorded for a few species while the majority remained unchanged. The remaining 14 lakes did not show noticeable changes over the 30-year period. Changes observed in the studied lakes did not follow a widely observed pattern in northern Hemisphere lakes. The results indicate that while climate change is a driving factor behind changing lake dynamics with increasing temperatures and decreasing lake ice cover duration, it cannot be the only force responsible.

Avainsanat - Nyckelord

Keywords: Palaeolimnology, Finnish Lapland, Climate Change, Diatoms

Säilytyspaikka - Förvaringsställe - Where deposited: E-Thesis

Viikki Campus Library

Muita tietoja - Övriga uppgifter - Additional information

Table of Contents

1. INTRODUCTION 4

1.1 Palaeolimnological approach 5

1.2 Diatoms 6

1.3 Original Study 7

1.5 Objectives of the study 7

2. STUDY AREA 8

2.1. Environmental characteristics 8

2.2 Site Descriptions 9

3 METHODS 10

3.1 Climate data 10

3.2 Sampling 10

3.3 Microfossil analysis 11

3.4 Data analysis 11

4. RESULTS 13

4.1. Regional climate Warming 13

4.2. Diatom species 14

4.3. Comparison between old and new species data 18

4.4. Diatom genera 19

4.5. Comparison between old and new genus data 21

5. DISCUSSION: 23

5.1. Climate 23

5.2. Diatoms 24

5.2.1 General diatom distribution according to vegetation zones 24

5.2.2 Observed changes over the past decades 25

5.3. The impact of climate warming on diatom communities 28

6. CONCLUSIONS 30

7. ACKNOWLEDGEMENTS 31

8. CITATIONS 32

9. APPENDIX 36

1. Introduction

Climate warming has increased during the last century, but especially over the last three decades, which, according to IPCC (2018) might have been the warmest of the last 800 years. Almost every year during the past decade new "records" of the warmest year have been broken. For example, 2014, 2015, and 2016 have all claimed the title of warmest year on record (Kennedy et al. 2016; Mann et al. 2016). Due to the strong feedback mechanisms, such as decrease in albedo and permafrost thaw, the Arctic is warming at twice the rate compared to the rest of the planet. Winter temperatures in northern boreal forest environments are expected to increase by 3 to 5^{o}C by 2050 (SWIPA 2017). In Finland, the normal period between 1981-2010 was 0.4 degrees higher than during the previous normal period (1971-2000), and 0.7 degrees warmer than during the normal period between 1961 and 1990 (Aalto et al. 2012). The warming appears to be stronger in the south of Finland than in the north, with highly variable seasonal patterns, and will have important consequences for land use, biodiversity, and overall physical environmental characteristics. Since the 1970s, climate models have been able to accurately predict the development of climate change up to the present time period (Hausfather et al. 2020). Today, modelling tools are getting increasingly complex and accurate at predicting future climate conditions. To test and challenge these models, other approaches - such as palaeoecological tools - should be used to reconstruct past environmental conditions, to understand natural long-term variability and to provide data against which climate models can be hindcasted (Smol 2009). In this aspect, lakes in northern high latitudes are especially important to study as they are sentinels of climate change. Their remoteness and lack of anthropogenic influences make them a prime target to observe direct climate and environmental changes. In their 2001 study, Weckström and Korhola (2001) were already expressing concerns about the increasing impacts that climate warming would have on ice cover duration and growing season in Arctic and subarctic lakes.

Over the past decades, many studies focusing on the environmental history of northern Fennoscandia have been conducted on lake sediments. Firstly, due to high lake density, with highest density values over 1000 lakes/100 km2 in Finnish Lapland (Tikkanen 2002), and secondly, because these lake archives consisting of biota remains are important tools to reconstruct

environmental conditions qualitatively and quantitatively. In the late 1990s, many studies describing either the chemical characteristics of lakes, or interaction between lake biota and various environmental factors were published (Weckström et al. 1997a, b; Blom et al. 1998; Korhola 1999). Due to the rapidly increasing rate of changes, these studies could be followed up to better understand the magnitude of these changes at a regional scale.

1.1 Palaeolimnological approach

Palaeolimnology is the study of past aquatic ecosystems including freshwater, brackish waters, and saline lakes. It is used to reconstruct past ecological conditions of lakes, from aquatic communities to physico-chemical conditions and their interactions (Smol 2009). Sediments are continuously accumulating into lakes and if the sedimentation conditions are optimal, lake sediments are a book of environmental history in a chronological order (Cohen 2003). The sediment material originates from a large variety of sources within the drainage basin (catchment area), making it a very rich source of information on the surrounding environmental conditions (Smol 2009). The general stability of the sediment input makes it ideal to reconstruct how conditions might have evolved over time. The biological remains of different organisms can be used as indirect (proxy) tools in environmental reconstruction (Cohen 2003). Knowledge of the ecology of the modern biota in the study area enables the use of lake sediment series incorporating some of these biotas, where changes in species composition within the sediment record will reflect changes in environmental conditions. The choice of the study area is important as sufficient understanding of the local processes is needed to better understand any potential variations in environmental conditions (Smol 2009). Once the study sites have been selected, each lake needs to be sampled at the optimal location regarding the sedimentation processes (i.e. the sedimentation basin) so that the sediment archive is the most representative of its surroundings (Reeves 2014).

With the continuous development of computer technology and statistical tools, marked progress has been made on how data can be analysed. During the past decades, multivariate numerical techniques have become a standard procedure in palaeolimnological studies. Direct gradient analysis techniques such as canonical correspondence analysis (CCA) can be used to detect patterns in species data and relate them to measured environmental variables controlling

their distribution (ter Braak 1986). To do so, the topmost 0.5-1 cm of the sediment representing the most recent years is collected from each lake and the environmental variables of interest are measured at the same site. After identifying and counting the biota of interest, multivariate statistical analysis methods are used to determine which of the measured environmental variables are statistically the most significant in explaining the species distribution and how the species are positioned along environmental gradients**.**

1.2 Diatoms

Diatoms are unicellular siliceous microscopic algae, which appear everywhere where sufficient light and moisture are available for photosynthesis. They are responsible for 45% of Earth's global primary production and therefore play a critical role in the functioning of aquatic ecosystems (Werner 1977; Benoiston et al. 2017). Due to their silica shell, or frustule, diatoms are generally well preserved in sediments and identifiable to the species or even subspecies and variety level. Their distribution is controlled by many ecological factors such as temperature, pH, nutrients or salinity, to which they are very sensitive (Stoermer and Smol 1999). Their short life cycle coupled with their narrow optima and tolerance to many environmental variables make them an excellent tool to observe and reconstruct past environmental conditions, and they are one of the most commonly employed palaeobioindicators (Moser et al. 1996).

Diatom frustules are composed of two separate valves (epitheca and hypotheca), and a number of girdle bands holding the valves together. Identification of diatoms is based on the shape and various species-specific characteristics of the siliceous valves. They can be divided into two major groups according to their overall shape: centric and pennate diatoms (Stoermer and Smol 1999). Centric diatoms are mostly cylindrical and are often radially symmetric relative to the pervalvar axis, while pennates are elongated, with lateral symmetry (Patrick and Reimer 1966). Diatoms reproduce by cell division where each daughter cell will receive one original valve from the parent cell. The successive division of cells leads to a continuous reduction in size of the bottom valve, while the top valve will keep its size. This shrinkage will continue until the cell is too small to divide any further, in which case it is able to reproduce sexually to restore the cell to the original size (Round et al. 1990). Diatoms can be classified under two major groups according to their habitat: planktic and benthic diatoms. Planktic species are floating freely in the water column,

while benthic species live near the bottom of lakes and can be attached to the substrate. Within this benthic habitat group, species can be further subdivided according to their preferred growth habitat, such as epipsammic (attached to sand), epilithic (attached to stones/rocks), and epiphytic (attached to plants), showing their variability towards specific environmental conditions.

1.3 Original Study

Weckström and Korhola (2001) aimed to explore relationships between diatom assemblage composition and species richness, and environmental variables in lakes in subarctic Lapland, with particular attention to air temperature. Their data was collected in July 1995 and 1998 from 64 lakes in Northwestern Finland. Surface sediment samples as well as 22 geographical and physico-chemical environmental variables were measured from each lake. They concluded that temperature, lake water pH, calcium, sediment organic content, and total organic carbon were the most influential variables determining the distribution of diatoms in the area (Weckström and Korhola 2001). Furthermore, air temperature was identified as one of the strongest external variables explaining variations in the diatom data. Temperature can impact diatoms either directly by stimulating their metabolic processes but also indirectly by altering water quality, lake stratification and various catchment factors.

1.5 Objectives of the study

The main objective of this thesis is to study the impact of recent climate warming on diatom communities in NW Finnish Lapland by:

1. comparing recent diatom communities of 26 subarctic lakes with diatom communities sampled from the same lakes by Weckström and Korhola (2001) ca. 25 years ago, and by
2. evaluating the role of temperature and other environmental variables as drivers of the possibly observed changes

2. Study area

The 26 lakes of the study are located in Northwestern Finnish Lapland (67°51'-69°10'N and 20°39'-24°10'E; using the code WFL), except for one lake (WFL 26), which is located in Norway close to the Finnish border (Figure 1). The study area covers a long climatic and vegetational gradient. Northwestern Finland is ideal for studying the impact of climate warming on aquatic ecosystems as it has remained one of the most pristine European regions in terms of anthropogenic atmospheric pollution over the past 30 years (Hettelingh et al. 1992; WHO 2018; González 2020). The chosen lakes are located in an area where local anthropogenic catchment disturbance is very low, with little to no human activity.

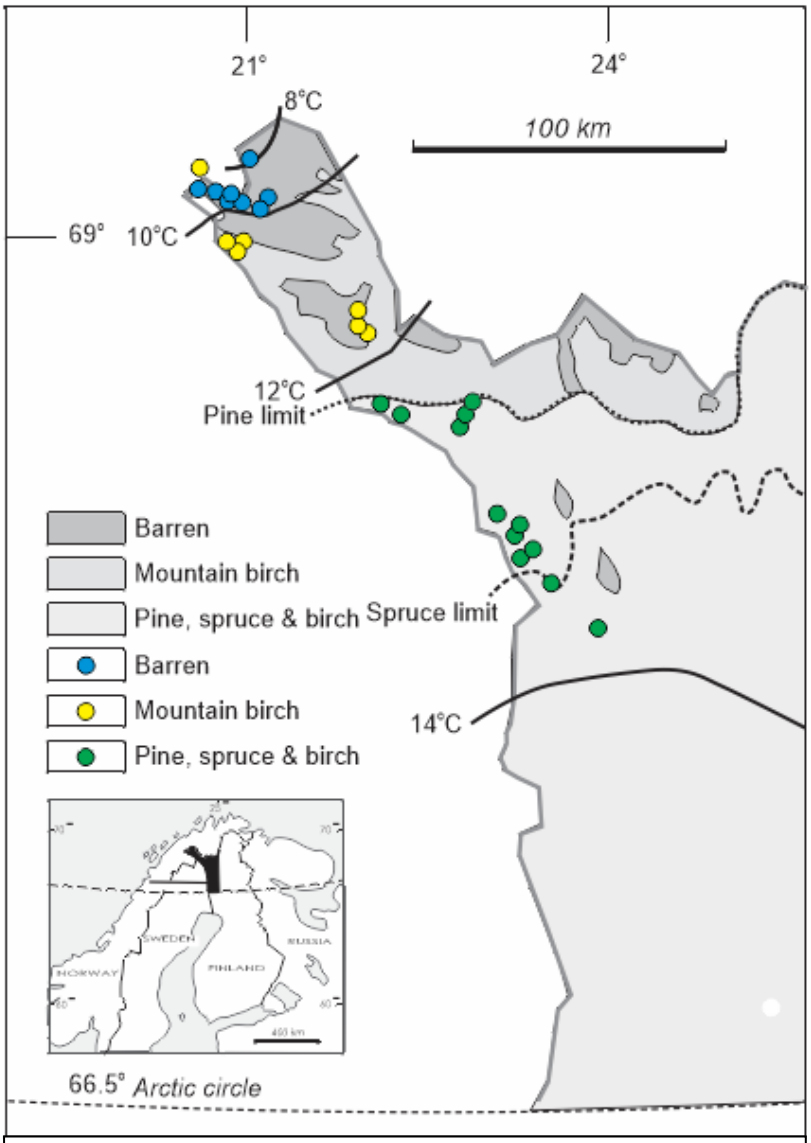

Figure 1: Map of the study area showing the location of the 26 lakes sampled. The isotherm of the mean july air temperatures (1961-1990) according to the original lake samples from 1995 (Weckstrom & Korhola 2001), and the main vegetation zones are displayed

2.1. Environmental characteristics

Most of the lakes in the area are unnamed and were therefore numbered following the same coding system as in the original dataset by Weckström and Korhola (2001). The mean annual temperature ranges from about -1.3°C in the north (Kilpisjärvi) to -0.6°C in the south (Muonio) (Finnish Meteorological Institute 2020). While the yearly average has remained quite steady during the past 30 years, the winter average

temperatures have been slowly rising, the month of June being the only period of the year experiencing cooling (Aalto et al. 2012). Current mean annual precipitation of 530 mm is consistent across the study area. This is a considerable change compared to the measured values in 1986 (Hämet-Ahti et al. 1988), which recorded 600 mm in both north and south, with a decline in the central region. The snow cover duration ranges from 225 days in the north to 200 days in the south (Merkouriadi et al. 2017). Snow acts as a long-term insulator for lake ice, increasing the duration of ice cover. The ice-free period ranges from May-June to October-November (Hämet-Ahti et al. 1988). However, recently the lakes have been freezing later and the ice has melted earlier (Korhonen 2019).

The bedrock in the area consists mainly of Precambrian orogenic plutonic rocks, but also karelidic schists occur (Simonen 1980). The bedrock is overall alkaline, which can lead to higher pH in some lakes.

The vegetation varies along the study transect from coniferous boreal forest in the south referred to as the pine, spruce and birch (SPB) vegetation zone, to mountain birch woodland (MBW), and finally to barren (Ba) ground in the north and high-altitude sites. The coniferous boreal forest is dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Hämet-Ahti et al. 1988). Many lakes in the southern part are surrounded by peatlands. The central study area is dominated by pine and birch forests due to its sandy terrain, while only mountain birch (*Betula pubescens* subsp. *czerepanovii*) grows in the north, with only a few pine trees in the sunny valleys. When reaching the northernmost region of the study area, the vegetation shifts drastically to treeless tundra consisting mainly of ground vegetation like lichens, willows and shrubs (e.g. *Salix spp.* and *Betula nana*).

2.2 Site Descriptions

The 26 lakes were selected from the original 64-lake data set described in Weckström & Korhola (2001). The northernmost area of the original data set was not sampled as thoroughly due to the remoteness and difficult accessibility of the lakes. The study lakes were selected on the basis that they were as pristine as possible, with minimal human influence. The physico-chemical

environmental variables (Appendix 2) have been collected as parts of multiple field campaigns throughout the years.

The 26 lakes sampled are small (mean area of 18 ha, range 0.9-70 ha), shallow (average depth 7 meters, range 1-25 m), mostly slightly acidic (mean pH of 6.4, range 5-7.5), and are characterised by low alkalinity and conductivity. Lakes in the barren area are very clear with secchi depth often exceeding the depth of the lake. Lakes in the MBW and SPB areas are characterised by lower secchi depth as their water is often brown due to the surrounding peatlands and larger input of humic substances.

3 Methods

3.1 Climate data

Looking specifically at how this warming trend has affected the study area of Northwestern Finnish Lapland, the past 30 years' climate was reconstructed, taking into account seasonality adjusted to the regional conditions (Figure 2). Weather stations from the south (Muonio) and north (Kilpisjärvi) of the study area were chosen to observe the magnitude of meteorological changes (Finnish Meteorological Institute 2020).

3.2 Sampling

The sediment samples were collected over two separate field sessions. Three lakes (WFL25, 26, and 27) were sampled during three days in August 2020 as part of the University of Helsinki Field course on Arctic ecosystems and climate. The remaining 24 lakes were sampled over the first week of September in 2020. One lake (WFL 10), however, was discarded due to the poor quality of the sample. The sampling was carried out from an inflatable boat from and the deepest point of each lake, which was located using a UWITEC water depth gauge. For each lake, one surface-sediment sample (0-2.5 mm) was collected with an HTH gravity corer (Renberg and Hansson 2008). The

sediments were stored in Minigrip plastic bags and kept dark and cool (4^{o}C) conditions until freeze-dried (Savant ModulyoD Freeze Dryer).

3.3 Microfossil analysis

Subsamples of dry sediment (ca. 0.1 g) were placed in a solution of H_2O_2 and heated at 90^{o}C for two to three hours until all of the organic matter was oxidised. A few drops of HCl (37%) were added to remove H_2O_2 and possible carbonates from the sediment. The diatom solutions were then centrifuged (4 min at 1500 rpm) and washed at least five times. Excess water was removed using a pipette and topped up with distilled water. The resulting diatom suspension was evaporated onto coverslips and mounted on glass slides with Naphrax. From each slide, at least 500 diatom valves were enumerated using Zeiss Axiocam 506 colour microscope at 1000X magnification. The nomenclature mainly follows Hartley et al. (1986) to remain consistent with the nomenclature used in the original study by Weckström & Korhola (2001). The identification of diatoms was mainly based on Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b).

3.4 Data analysis

Prior to statistical analysis the diatom data was organised to both the genus, and the species level as relative abundances (%). Since the present dataset is compared with the dataset from the original study (Weckström and Korhola 2001), some diatom species were merged or classified under an alternative name, to achieve a better level of consistency in the taxonomy. Environmental data was retrieved from the original study. Thus, the updated diatom data was compared to environmental gradients based on the original environmental data.

Detrended correspondence analysis (DCA) was performed to analyse the main patterns of variation in both diatom species and genus data. As the gradient length of the first axis for the species data was 4.4 standard deviation units (SD), a unimodal approach, namely DCA, was used in order to compare the similarity between the species of the original study and the current study. Diatom species with relative abundance of at least 5% in one of the 52 sediment samples (26

original samples and 26 current samples) were displayed (Figure 3). Species data were square-root transformed and rare species were down-weighted prior to statistical analysis. The same approach was repeated using diatom data at the genus level. Diatom genera with relative abundance of at least 2% in at least two of the 52 sediment samples were displayed (Figure 2). While observations of unidentified species (spp.) were excluded from the species analyses, they were included in the genus analysis.

Canonical correspondence analysis (CCA) was employed to reveal the relationship between the diatom data and the environmental variables. CCA was used as the length of the first axis in DCA was 4.5 SD, suggesting the use of a unimodal approach. Statistical significance was tested using Monte Carlo permutation test (999 permutations). Prior to the CCA, environmental variables were log(x+1) transformed, and three nominal variables were added for the vegetation zones as binary codes (0/1). Out of the original measured 20 environmental variables, 12 were chosen for the final statistical analyses after screening with Variance Inflation Factor (VIF). Environmental variables with VIF-values < 20 were included in addition to environmental variables with ecological importance. Species data from newly collected samples was plotted passively, as the environmental data could not be updated. Passive samples will not affect the analysis of species-environment relationship but will be plotted according to their species compositions along the defined species-environment biplot space. Species data were square-root transformed and rare species down-weighted prior to statistical analysis. The same method was repeated using diatom data at the genus level.

Relative frequency diagrams were performed at both species and genus levels, showing the relative abundance of specific species within each lake. For the species level analysis, diatom taxa with relative occurrence of at least 5% in at least one sample were displayed. At the genus level, diatom genera with relative occurrence of at least 2% in at least two samples were displayed. All multivariate analyses were performed using Canoco for Windows 5.01 (ter Braak and Šmilauer 2002) and the stratigraphical diagrams using C2 v.1.7.7 (Juggins 2007).

4. Results

4.1. Regional climate Warming

The magnitude of yearly temperature changes seems to be consistent between Kilpisjärvi and Muonio, with a slow, steady increase over the past three decades. However, some strong seasonal fluctuations can be observed in both ends of the gradient, with the fall months (September and October) experiencing the strongest warming.

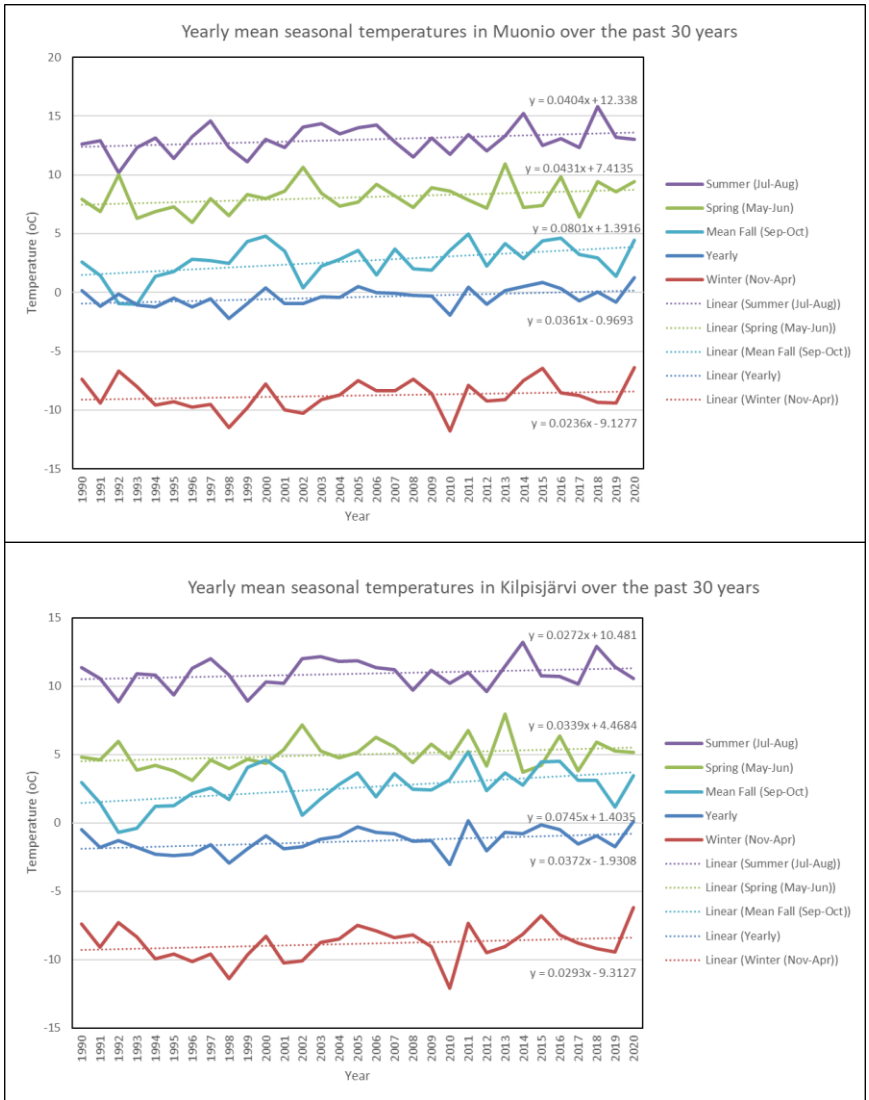

Figure 2: Weather data retrieved from the Finnish Meterological Institute's open database for both the Kilpisjarvi and Muonio weather stations. Yearly mean seasonal temperatures were calculated for the time period between 1990 and 2020.

4.2. Diatom species

A total of 185 diatom taxa representing 27 genera were recorded from the modern surface sediment samples of the 26 lakes. Out of the 185 diatom taxa, 28% occurred in only one lake, 78% occurred in less than 10 lakes, and only 22% occurred in 10 lakes or more. In addition, 42% of the species had a maximum abundance below 1%, and only 11% had a maximum abundance over 10% (Appendix 3).

	Eigenvalue		Cumulative Variance (%)	
Axis	DCA	CCA	DCA	CCA
1	0.439	0.465	12.5	14.5
2	0.221	0.241	18.9	22.1
3	0.173	0.214	23.8	28.8
4	0.093	0.159	26.0	33.7

Table 1: Species summary statistics

The first two axes of the species DCA accounted for 18.9% of the cumulative variation in the data (Table 1). The DCA analysis was performed to compare changes in diatom communities between the modern and older samples. It provides a side by side view of each lake allowing to evaluate potential changes in diatom assemblages between the current and past diatom communities depending on their proximity with one another along the DCA axes (Figure 3). The species DCA shows a clear delimitation by vegetation zones, with SPB lakes located on the center-left side (Figure 3). These lakes are defined by taxa such as *Eunotia rhomboidea, Pinnularia rupestris* and *Frustulia rhomboides* var. *saxonica*. Lakes of the MBW zone are clustered around the central area of the DCA, along with their typical species *Brachysira brebissonii*, *B vitrea*, and *Achnanthes pusilla.* The Ba lakes are located on the upper right side of Figure 3, hosting species such as *Aulacoseira distans*, *Achnanthes levanderi*, and *Cyclotella rossii*. These trends can also be seen in the relative abundance diagram (Figure 4).

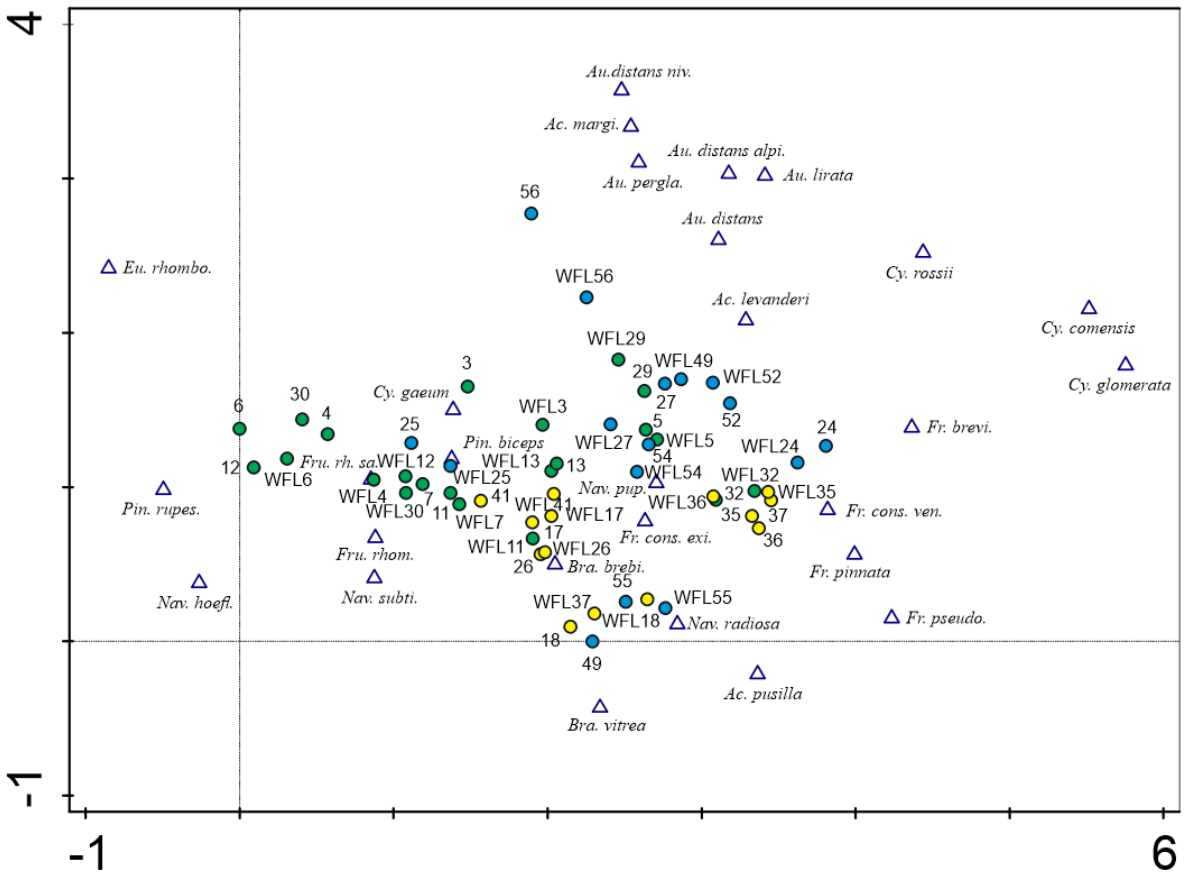

Figure 3: Detrended Correespondence Analysis (DCA) of diatom observations at the species level for the 26 study lakes. Points including the prefix WFL represent new samples; points without the prefix represent samples collected between 1995 and 1998. The colour of the dots representing the study sites refer to the vegetation zones: Green = SPB, Yellow = MBW, Blue = Ba. Explanations for the abbreviations can be found in Appendix 1.

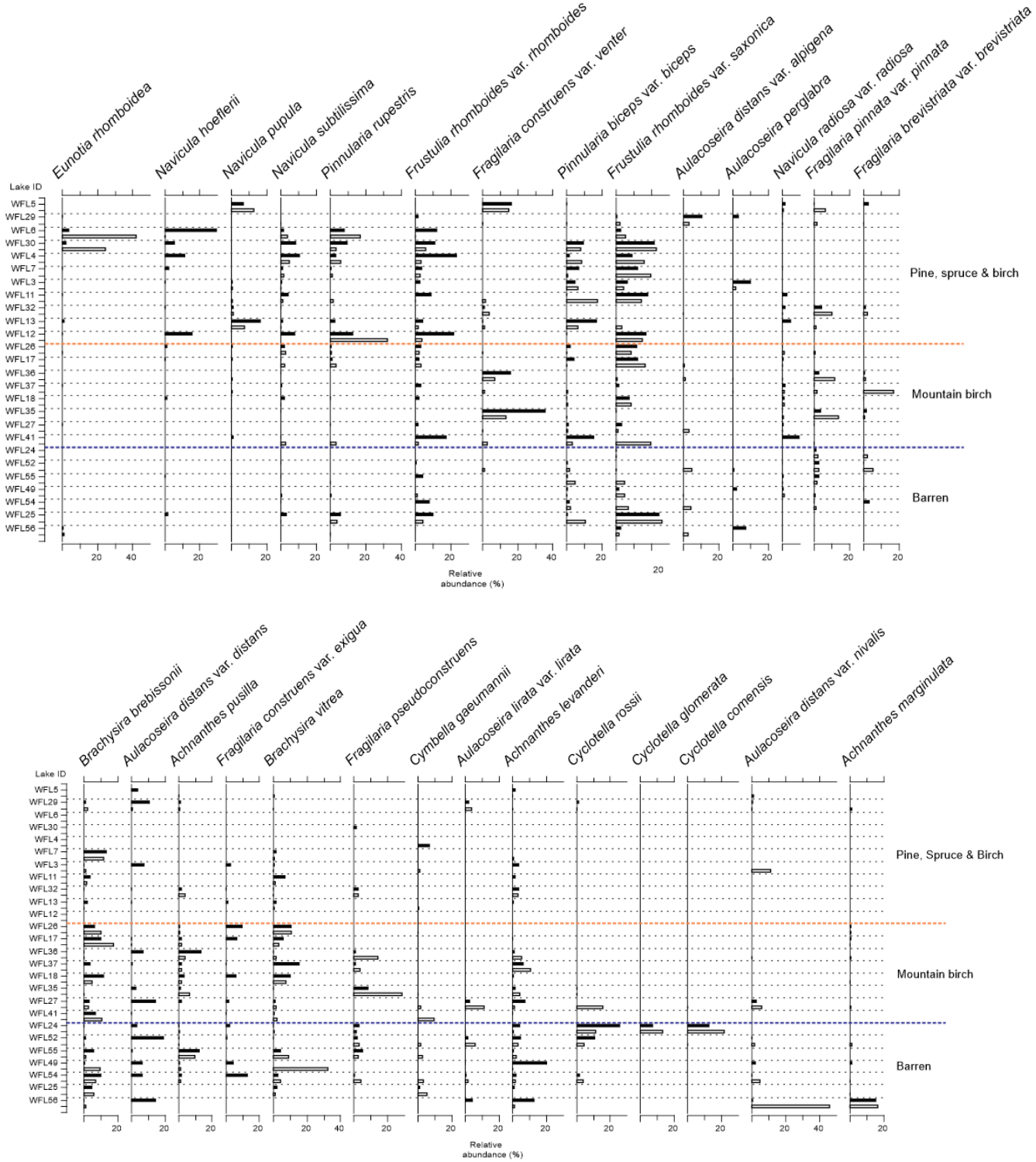

Figure 4: Relative frequency diagram of the dominant diatom taxa (>5% relative occurrence in at least one sample). For each lake, the 2020 (black bar) observation is on top of the samples collected between 1995 and 1998 (open bar) observation. Lakes are sorted from lowest (top) to highest altitude (bottom), which also coincides with their respective vegetation zones.

For the CCA, highly collinear variables were deleted according to their Variance Inflation Factors (VIF): variables with values above 20 were removed, leaving 12 environmental variables to be included in the analysis. Eigenvalues of the first two CCA axes were λ_1=0.465 and λ_2=0.241, representing 22.1% of the cumulative variance in the diatom species data. In the CCA biplots (Figures 5 and 8), taxa and genera data had to be plotted separately from the lake and environmental data due to the large difference in scale of the axes.

In the species CCA biplot (Figure 5), many of the lakes in the SPB vegetation zone are located in the upper right quadrant characterised by higher amounts of mire area (MireArea) in their catchment, higher temperature (AirT), comparatively high amounts of total organic carbon (TOC), and lowest water pH. Diatom taxa indicative of these conditions lie on the right-hand side of the biplot. Species like *Navicula hoeflerii* and *Eunotia rhomboidea* are found in a few lakes where pH values were the lowest. The MBW zone can be considered as a transitional environment or ecotone between the Ba and the SPB regions. Lakes in this zone are mostly scattered on the lower half of the CCA biplot. These lakes have a large size and depth gradient and have elevated conductivity like the Ba lakes, but are cooler, more alkaline, and have higher pH values than the SPB lakes. Lakes in the Ba region are mostly located on the left-hand side of the biplot. These lakes are typically colder, deeper, and larger with low TOC concentrations. Diatom taxa on the top left quadrant are typically found in these lakes. Species such as *Frustulia rhomboides* var. *rhomboides*, *Frustulia rhomboides* var. *saxonica*, *Brachysira brebissonii*, or *Pinnularia biceps* were found consistently across the dataset, disregarding of the vegetation zone. On the other hand, species like *Cyclotella glomerata* and *Cyclotella comensis* were only found in one lake (WFL 24), which was the deepest lake of the dataset. Looking at the CCA biplot, it is also possible to observe along which environmental gradients changes between samples have occurred (see next chapter). As an example, looking at lake WFL 30, the changes are happening very clearly along the LOI, TOC, and pH axis.

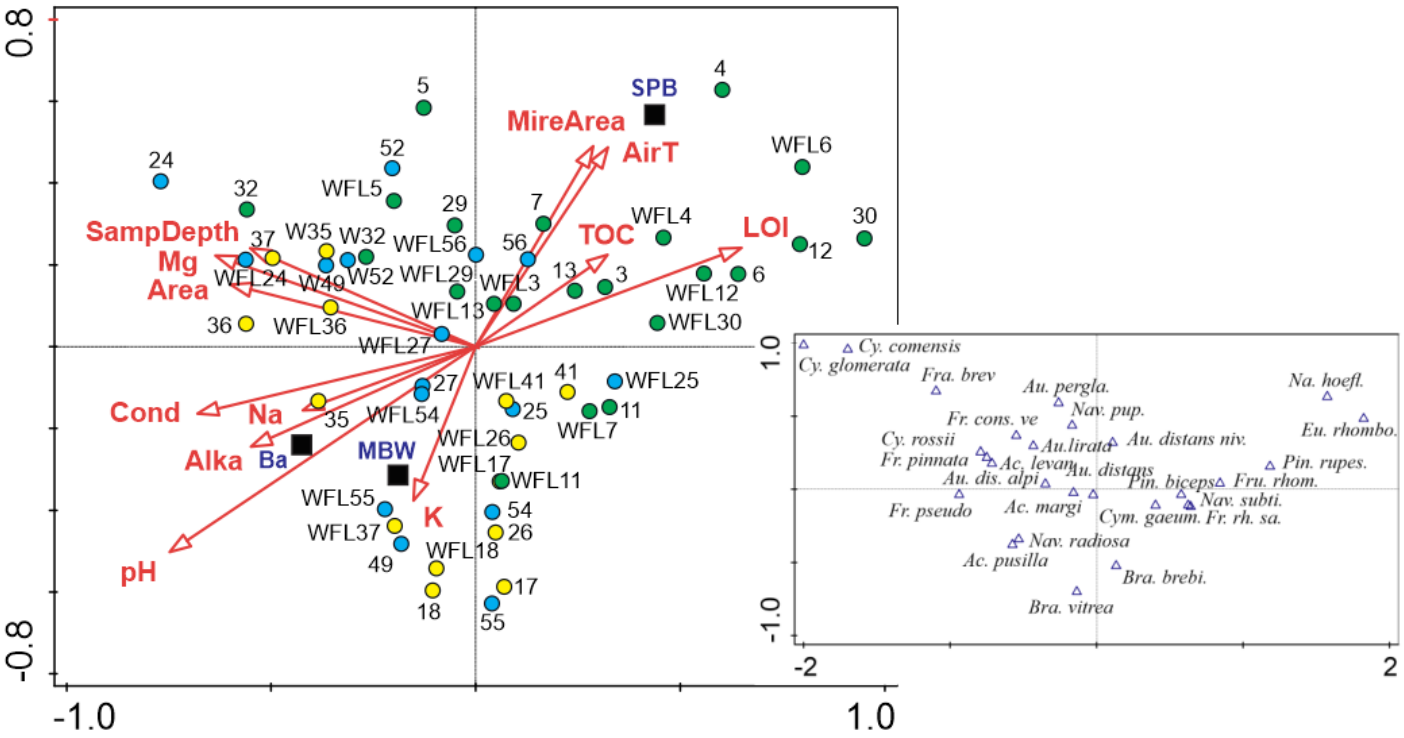

Figure 5: Canonical Correespondence Analysis (CCA) ordination diagram showing the relationship between diatom observations and selected environmental variables. Points including the prefix WFL represent new samples; points without the prefix represent samples collected between 1995 and 1998. The qualitative variable of vegetation zones (SPB, MBW, Ba) was included passively and is labeled with squares. The colour of the dots representing the study sites refer to the vegetation zones: Green = SPB, Yellow = MBW, Blue = Ba. Explanations for the abbreviations can be found in Appendix 1.

4.3. Comparison between old and new species data

In general, the 26 lakes can be categorised into three groups based on changes in conditions since 1995: large, moderate, and negligible (according to the distance between site symbols in Figure 3). WFL 49 seems to have undergone the largest changes with a marked shift in dominant species. In the original study the lake diatom assemblages were dominated by *Brachysira vitrea*, which was completely absent in the current sample, where instead *Achnanthes levanderi* has become dominant. WFL 30 experienced a large decline in the percentage abundance of *Eunotia rhomboidea*, which was rare in the current sample, in favour of species such as *Navicula hoeflerii* and *Navicula subtilissima*. WFL12 had a large increase in *Frustulia rhomboides* and *Navicula hoeflerii* from low relative abundances to the current ca. 20% abundance. On the other hand, the

relative abundance of *Pinnularia rupestris* decreased by half, from 30% to 15%. Finally, WFL37, which was earlier dominated by species such as *Fragilaria brevistriata*, has shifted towards the dominance of *Brachysira vitrea*, which was absent in the original samples. Eight of the lakes have undergone moderate changes; WFL3, 4, 6, 11, 18, 27, 41, 56. In most of these lakes the change occurred only between a few species, often marking a turnover of specific taxa, whereas the majority of other species remained similar between the old and current samples. For example, WFL6 had a noticeable switch from the original *Eunotia rhomboidea* dominance to *Navicula hoeflerii.* Another example is WFL11, with the absence of *Pinnularia biceps* in the newer samples. The remaining 14 lakes (WFL 5, 7, 13, 17, 24, 25, 26, 29, 32, 35, 36, 52, 54, and 55) show negligible to no differences between the original and the recent samples.

4.4. Diatom genera

A DCA was also performed at the genus level (Figure 6) to observe more general changes in lake diatom communities. The first two axes of the genus DCA accounted for 29.3% of the cumulative variation in the data (Table 2).

	Eigenvalue		Cumulative Variance (%)	
Axis	DCA	CCA	DCA	CCA
1	0.236	0.221	28.1	25.8
2	0.093	0.085	39.3	35.8
3	0.048	0.063	44.9	43.2
4	0.027	0.042	48.1	48.1

Table 2: Genus summary statistics

Similarly to the species DCA, the genus DCA shows a clear delimitation by vegetation zones. SPB lakes are on the the left side of the figure (Figure 6), defined by genera such as *Frustulia, Eunotia* and *Pinnularia*. Lakes of the MBW zone are clustered on the central upper side of the figure, associated with genera like *Brachysira* and *Fragilaria*. The Ba lakes are spread across the right side of the plot, with frequent occurrence in samples of genera such as *Achnantes*, *Aulacoseira*, and *Cyclotella*. Genera such as *Cymbella* and *Nitzschia* are evenly found throughout the three vegetation zones.These trends can also be clearly observed in the genus relative abundance diagram (Figure 7).

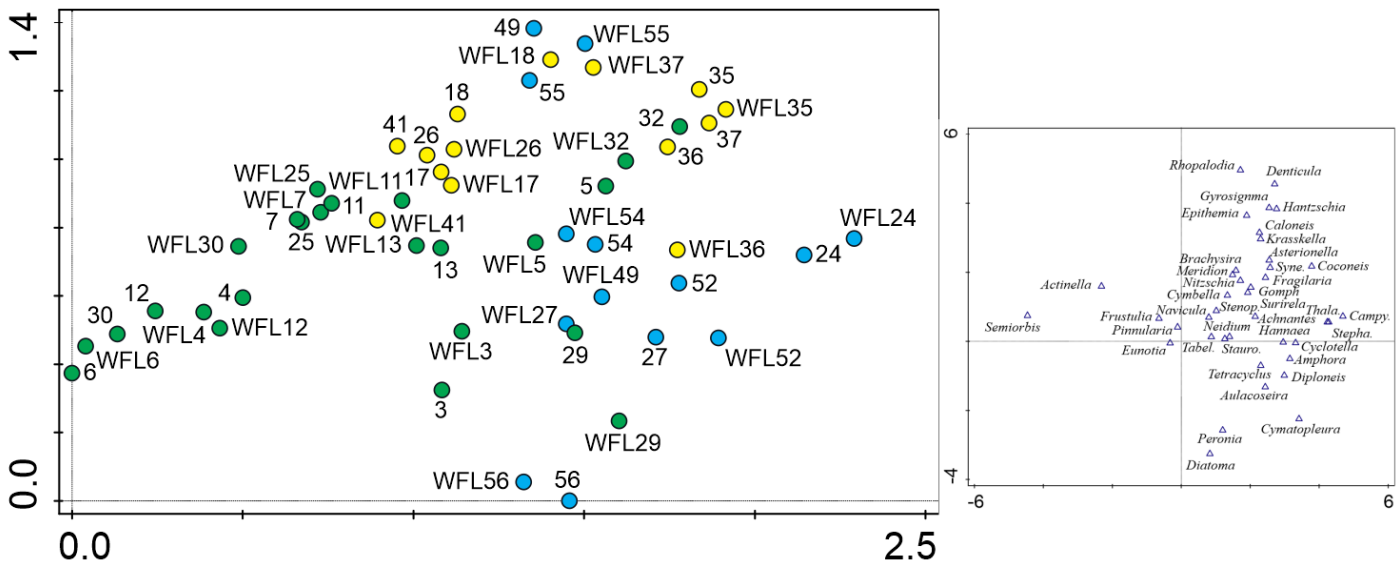

Figure 6: Detrended Correespondence Analysis (DCA) of diatom observations at the genus level for the 26 study lakes. Points including the prefix WFL represent new samples; points without the prefix represent samples collected in 1995 and 1998. The colour of the dots representing the study sites refer to the vegetation zones: Green = SPB, Yellow = MBW, Blue = Ba. Explanations for the abbreviations can be found in Appendix 1.

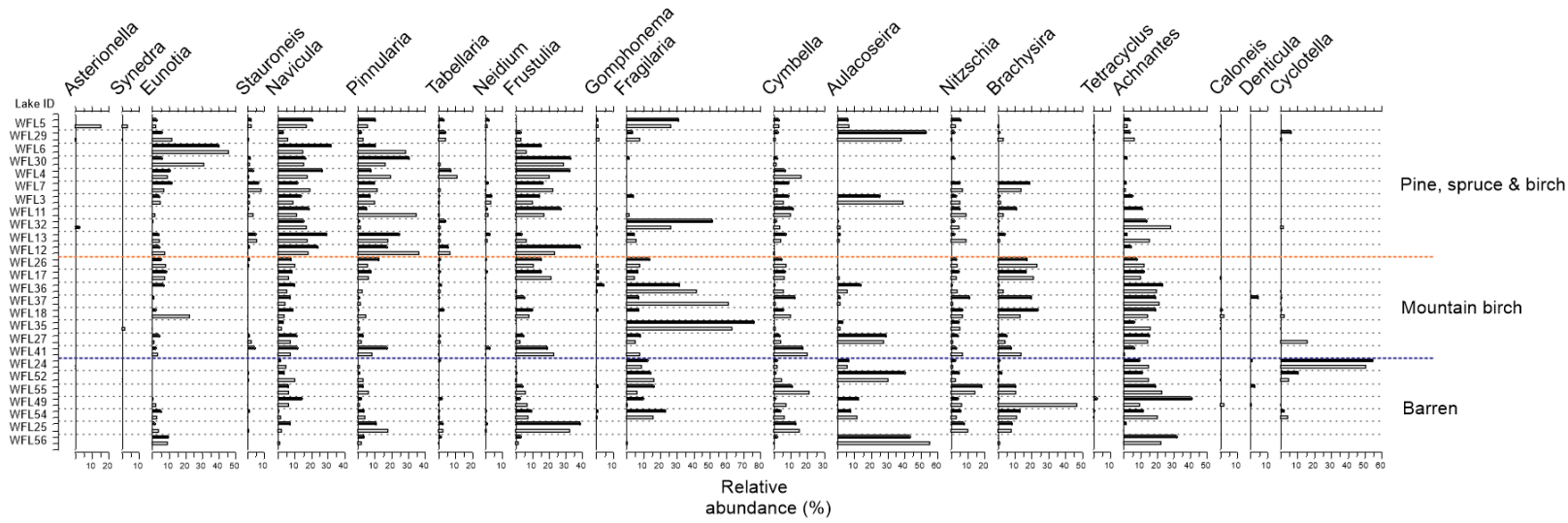

Figure 7: Relative frequency diagram of the dominant diatom genera (>2% relative occurrence in at least two samples). For each lake, the 2020 (black bar) observation is on top of the 2001 (open bar) observation. Lakes are sorted from lowest (top) to highest (bottom) altitude, which also coincides with their respective vegetation zones.

For the genus CCA, eigenvalues of the of the first two CCA axes were λ_1=0.221 and λ_2=0.085, representing 35.8% of the cumulative variance in the diatom genus data. From the CCA biplot (Figure 8), the separation between vegetation zones is clearer than at the species level, making it possible to differentiate between Ba (top left quadrant) and MBW (bottom left quadrant). The ecological and environmental conditions attributed to each vegetation zone do not differ from the species level analysis. In the CCA biplot, lake WFL 24, located in top left quadrant, clearly differs from the other lakes. Diatom genera associated with this lake are *Stenopterobia* and *Thalassiosira* with very low abundances. Genera such as *Cyclotella* and *Aulacoseira* are indicators of the deep lakes located in the Ba zone. The acidic, humic conditions attributed to lakes in the SPB zone can be linked to genera rare in this data set such as *Actinella* and *Peronia*. While genera such as *Navicula*, *Pinnularia*, and *Eunotia* are present in all three vegetation zones, they are overall more abundant in the SPB area. The genus *Tabellaria* appears to be a good indicator for lakes in mire areas. As for MBW lakes, the genera *Denticula, Epithemia and Rhopalodia* seem to be a good indicator of their high alkalinity.

4.5. Comparison between old and new genus data

While some of the lakes seemed to have experienced large changes at the species level, the magnitude of some of these changes tends to be more discrete at the genus level. For example, clear differences in the species relative abundance diagram of WFL 6 are not reflected in either of the DCA analyses or in the genus relative frequency diagrams. Inversely, some changes are more obvious at the genus level. This can be seen in Figure 7 for both WFL 49 and WFL 37, which already experienced substantial changes at the species level. In WFL 49, *Brachysira*, which was the dominant genus in the original sample, is almost completely absent from the recent sample. Similarly, *Aulacoseira* occurred in the recent sample but was not found in the earlier observations (Figure 7). In WFL 37, the genus *Fragilaria* largely dominated the original sample with a relative abundance of over 60%, whereas its current abundance is as low as 10%, mostly replaced by *Brachysira*. Some changes that were not observed at the species level were evident also in lake WFL 18, where a high relative abundance of about 25% of *Eunotia* decreased to below 5%, whereas *Fragilaria* appeared in the new sample having been absent in the original.

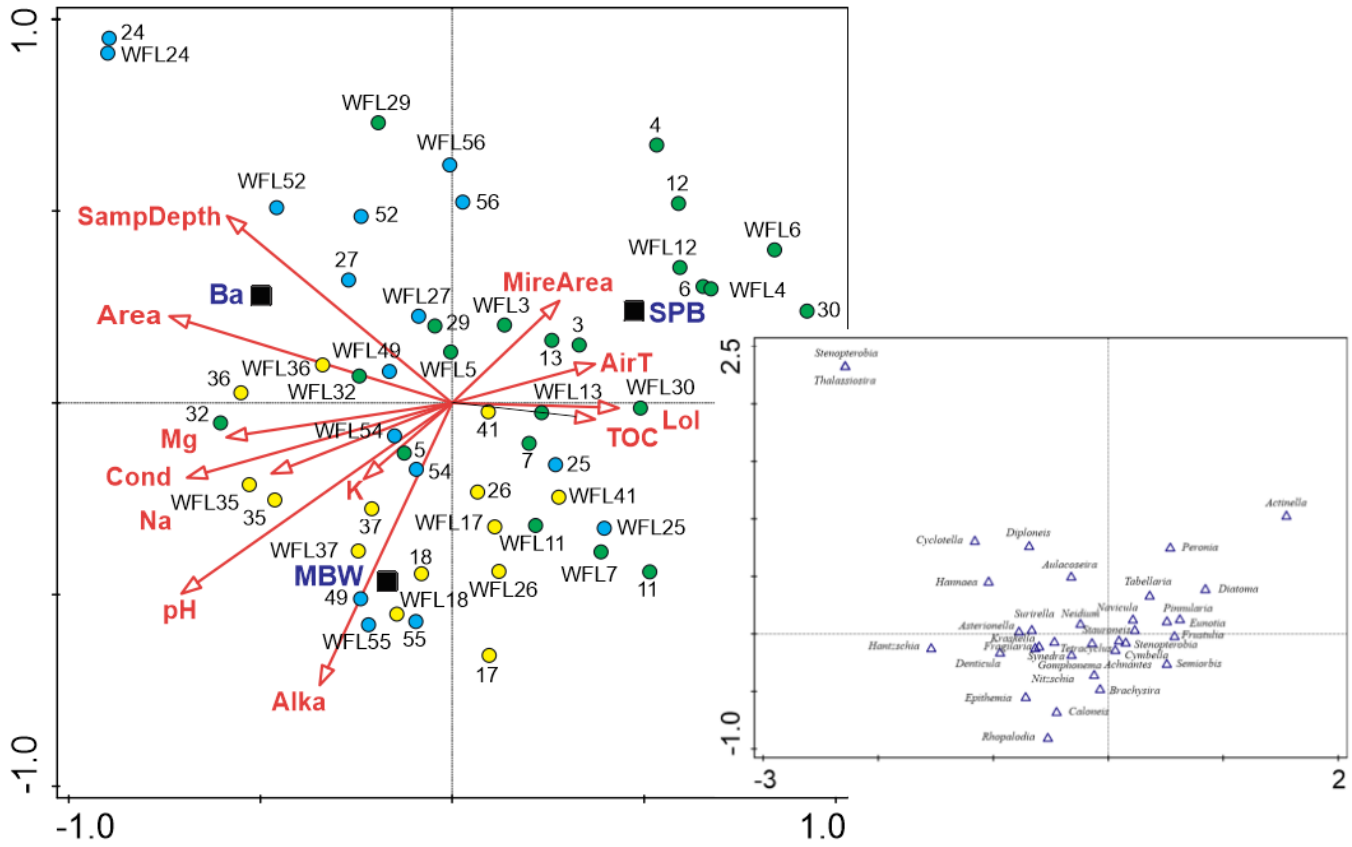

Figure 8: Canonical Correespondence Analysis (CCA) ordination diagram showing the relationship between the diatom observations and the selected environmental variables. Points including the prefix WFL represent new samples; points without the prefix represent samples collected in 1995. The qualitative variable of vegetation zones (SPB, MBW, Ba) was included passively and is labeled with squares. The colour of the dots representing the study sites refer to the vegetation zones: Green = SPB, Yellow = MBW, Blue = Ba. Explanations for the abbreviations can be found in Appendix 1.

5. Discussion:

5.1. Climate

Over the past 30 years, climate has been steadily warming in the study area as shown in Figure 2 (Finnish Meteorological Institute, 2020). However, it is critical to note that fluctuations in temperatures observed cannot be attributed to climate change alone. Changes and improvements in the accuracy of the climate data, combined with an increased frequency of data collection and continuous monitoring of weather stations might play a role in explaining small variations in the regional temperature record (Aalto et al. 2012). Instead of observing the annual temperature only, it is crucial to separate the seasonal trends of climate warming, as these may be of higher importance in shaping the structure of subarctic ecosystems. During the past 30 years, each season has undergone continuous increases in temperature, with the fall months (September and October) experiencing the strongest warming. This continuous warming, combined with the increase in the frequency of extreme events - such as storms, heavy rainfall and heat waves - has had a strong impact on factors such as the ice cover dynamics of lakes (Gebre et al. 2014; Filazzola et al. 2020). Over the past century, ice break-up and ice freeze-up trends in Finnish lakes have varied by about 4-10 days, reducing the ice cover duration by 11-17 days (Korhonen 2019). A climate model by Gebre (2013) looking at lake ice phenology in the Nordic and Baltic regions of northern Europe has predicted that by 2041, ice freeze-ups are expected to be delayed by 1-3 weeks, while ice break-ups are expected to occur 1-10 weeks sooner, cumulatively reducing the overall ice duration by 1-11 weeks. All of these changes in ice dynamics will have important impacts on the seasonal variability of lake processes. This was nicely demonstrated by Sharma et al. (2019), who studied two Swedish lakes that exceptionally did not freeze over during the winter. Internal processes in these lakes were disturbed due to the increase of surface temperatures, which in turn led to increased primary production and algal biomass (Sharma et al. 2019). While shifts in the duration of ice cover are an important driver of many lake processes, increasing temperatures could impact aquatic ecosystems in many other ways. Higher temperatures could also be reflected by increased stratification of lakes, changing their mixing regime and circulation of nutrients (Havens and Jeppesen 2018; Woolway and Merchant 2019). These changes, associated with longer growing seasons, could have cascading effects on the food web of the lakes (Havens and Jeppesen 2018).

Changes in precipitation patterns tend to affect erosion around lakes, with more precipitation generally translating into higher inputs from the catchment, increasing organic carbon and nutrients (Vincent et al. 2013). Longer growing seasons and thawing of permafrost may lead to a northward migration of vegetation, possibly reaching previously treeless tundra regions (Garamvoelgyi and Hufnagel 2013). Migration of vegetation to these previously treeless areas could affect erosion in the catchment, as well as input of humic substances to lakes, leading to potential browning of these clear-water lakes.

5.2. Diatoms

Large environmental gradients commonly result in low occurrence and abundance of many diatoms species. This is consistent with the results of the current study, where 78% of species occurred in less than 10 lakes. These large gradients enable the potential for turnover in species compositions and increase heterogeneity of the data (Pienitz et al. 1995; Birks 1998). A total of 185 species representing 27 genera were identified from the 26 lakes studied (Appendix 3). In comparison, Weckström and Korhola (2001) observed 370 species from 40 genera within the 64 lakes of their study. While this could initially be interpreted as a large decrease in species diversity, it is most likely a result of a smaller sampling size and, to a much lesser extent, due to some remaining identification differences after taxonomic harmonization of the data sets. The presence of two different analysers for diatom identification and counting might have resulted in small-scale inaccuracies in the data, which were an additional motivation behind the statistical analyses at the genus level. While species-level observation tends to provide more accurate results of changes in lake ecology, the main purpose of the genus level observations is to assess larger scale changes in overall diatom communities (Bennett et al. 2010).

5.2.1 General diatom distribution according to vegetation zones

The 26 lakes were divided between three distinct vegetation zones, all reflecting different ecological conditions and water chemistry. The CCA analysis allowed for a direct interpretation of which characteristics where the most representative of each vegetation zone, highlighting their

most impactful ecological conditions. The SPB region was defined by its higher temperature (AirT), comparatively high rates of total organic carbon (TOC), and relatively low water pH. The most dominant diatom taxa in the area verified this observation with taxa such as *Eunotia rhomboidea* and *Pinnularia rupestris* generally indicating warmer lowland lakes, which are slightly acidic. At the genus level, these conditions were associated with *Actinella* and *Peronia*. As only one valve of these genera were found in one lake, their indicator value in this study is limited. The MBW vegetation zone is a transition zone between the SPB and Ba regions. This is also suggested by the species distribution, as MBW seemed to have the highest diversity (Weckström and Korhola 2001), including many diatom taxa that can be commonly found in both of the other vegetation zones. In all statistical analyses, MBW lakes showed a wider distribution, partly overlapping with the other vegetation zones. In the Ba region, colder, deeper, larger lakes were dominant, with low TOC concentrations. The clear spread of Ba lakes along the depth gradient on both species and genus CCA analyses (Figures 5 and 8) suggests that higher water depth is a common characteristic for these lakes. The dominant genera observed in these lakes seem to support this, as planktic species such as *Cyclotella* and *Aulacoseira* favour deeper water with elevated turbulence (especially in the case of *Aulacoseira*). Going back to the example of WFL 24, it contained many unique species (e.g. *Cyclotella glomerata* and *Cyclotella comensis*) and genera (e.g. *Stenopterobia* and *Thalassiosira*), which are good indicators for showing that it is the deepest lake of the dataset.

5.2.2 Observed changes over the past decades

In general, the trends in diatom communities analysed in this study remained similar to the observations made by Weckström and Korhola (2001). A majority (14/26) of the 26 lakes did not show clear changes in diatom composition, indicating that lakes in the study area have not experienced any major turnover in water chemistry or other environmental variables despite changes in air temperatures and lake ice cover duration. Still, 12 of the 26 lakes were shown to have sustained some level of changes, with four lakes experiencing large changes, and eighth lakes experiencing moderate changes.

Of the lakes that experienced large changes in diatom communities, one was in the Ba vegetation zone (WFL 49), one in the MBW vegetation zone (WFL 37), and two in the SPB vegetation zone (WFL 12 & WFL 30). These lakes are located along the climate and vegetational gradient and reflect varying lake characteristics and ecologies, signifying that observed changes were not regionally focused. In lake WFL 30, a switch from *Eunotia rhomboidea* to *Navicula hoeflerii* and *Navicula subtilissima* was observed. While these three species seem to reflect similar ecologies (i.e. slightly acidic waters), the species CCA analysis shows a very clear gradient along the LOI, TOC and pH axes between the old and the new sample (Figure 5). This would indicate a lowering in LOI and TOC values, combined with a higher pH. Along this same LOI, TOC and pH gradient in the species CCA, lake WFL 12 showed marked changes with a large increase in *Frustulia rhomboides* and *Navicula hoeflerii*, associated with a clear decrease in *Pinnularia rupestris*. However, when looking at both CCA analyses at the genus level, these changes were not reflected by any important ecological turnover. Lakes WFL 37 and WFL 49 are in different vegetation zones (MBW and Ba, respectively) and vary highly in their size, depth, and altitude. Yet they display similar ecological conditions with neutral pH (7-7.3) and relatively high alkalinity (8-9.5 mmol/l). These are the two lakes with the largest changes in their diatom compositions (genus *Brachysira*), occurring along the same environmental gradient (in opposite directions) according to the species CCA. Lake WFL 37 showed a large increase in *Brachysira vitrea* and *Brachysira brebissonii*, with a cumulative relative abundance of 20% in the modern sample compared to no occurrences in 1995. On the other hand, lake WFL 49 experienced the opposite trend, with a reduction in cumulative relative abundance of these species from 47% in 1995 to approximately 1% in the modern sample. *Brachysira vitrea* is known to thrive in oligotrophic, alkaline waters (Wolfel and Kling 2001), conditions that occur in both of these lakes. The environmental gradient along which the change occurs in these two lakes is not well captured by the variables available in this study. This could mean that changes in diatom communities could be attributed to other physical or chemical variables or even changes in the benthic habitat of the lakes. Most of the observed changes in the study lakes appear to be occurring in benthic diatom communities. Planktic diatoms appear to be rather insensitive to direct temperature changes, but instead seem dependent on processes like turbulence, light, or nutrient supplies, which ultimately are controlled by climate (Anderson 2000). In temperate lakes, this causes planktic diatoms to generally bloom in the spring when the conditions favour plankton growth (Reynolds 1984). However, with the

changing ice and temperature dynamics, especially with the fall months being warmer, the nature and timing of diatom responses may vary (Rühland et al. 2015). It might also become more frequent for lakes to experience a peak in biomass in the autumn. This trend of peak autumn biomass was previously observed in lake Saanajärvi (WFL 24) by Rautio et al. (2000).

Regarding the lakes with moderate changes, four of them were located in the SPB vegetation zone, three in the MBW vegetation zone, and one in the Ba region, overall showing a more pronounced geographical pattern than the larger changes. One example from the SPB region is WFL 6. When looking at both CCA biplots (Figures 5 and 8), it is clear that changes are happening along the AirT and MireArea/pH gradients, indicating an increase in the air temperature and/or higher amounts of mire area in the lake catchment. However, this lake has crystal clear water with large water moss areas in the bottom, and very little mire in its catchment. As the mire area in the lake catchment is small, this change could have more to do with increased air temperature and changes in seasonality. In the MBW zone, lake WFL 18 showed moderate changes in species and genus composition in both relative frequency diagrams and DCAs, but this was not reflected in the CCAs. Overall, with two lakes having experienced large changes and four lakes with moderate changes, the SPB vegetation zone showed the largest difference to the original study. Due to its lower altitude compared to the other two vegetation zones, it is very likely that these lakes have been impacted the most by increasing temperatures and resulting changes in algal communities and primary production, despite the somewhat complex response of the diatom communities in these lakes

For both studies, sediment samples were collected from the deepest point of each lake. The purpose of sampling the deepest point is to obtain a sample from the accumulation zone of the lake, providing the most complete archive of the basin's sedimentation (Smol 2009). If one of the samples was taken on a flat central basin, and the other taken on a slight slope, it could have an impact on quality and quantity of the fossil remains in the sediment record. In addition, lakes in the SPB and MBW areas tend to have overall faster and steady sedimentation rates due to more vegetated catchment areas combined with higher productivity with warmer temperatures, providing higher OM flux and faster erosion rates compared to Ba lakes (Johansson 1985; Rekolainen et al. 1986). Thus, observations made for the SPB and MBW lakes could be more consistent with the aims of this study to compare two distinct samples from different time periods.

Lakes in the Ba region tend to have much lower sedimentation rates (Korhola and Weckström 2004; Frolova et al. 2018). This increases the risk that not enough new sediment has accumulated in 25 years on top of the reference sample. Thus, it could be possible that the recent surface sample (2.5 mm) also contains sediment from the reference sample. On the other hand, although their sedimentation rates are lower, the Ba lakes are deeper and their sediment contains less water, which decreases the possibility of the surface sample mixing with deeper layers. Overall, out of the 14 lakes that were considered to have experienced negligible changes, five were from the Ba vegetation zone. Considering that only 7 lakes were sampled in the Ba zone, a large majority of these lakes have not experienced noticeable changes over the past 25 years. While it is plausible that the more southern and lower-lying lakes in the SPB zone show earlier signs of warming compared to the lakes in the Ba zone, this lack of change in the Ba lakes could be due to overlap between the old and new samples.

5.3. The impact of climate warming on diatom communities

Over the past decades, a large number of studies have been published, aiming to observe shifts in diatom communities as a result of recent climate warming (e.g. Battarbee et al. 2002; Rühland et al. 2003, 2008, 2015; Rühland and Smol 2005; Winder et al. 2009). In many of these studies, sediment records dating back to pre-industrial time were analysed to observe long-term changes. A common trend observed during the last decades is the significant increase in the relative abundances of the genus *Cyclotella*, associated with a decline of the genus *Aulacoseira* and *Fragilaria* (Battarbee et al. 2002; Rühland et al. 2003, 2008; Rühland and Smol 2005). Climate warming, a longer growing season, and longer ice-free periods will generally favour planktic diatom species such as the genus *Cyclotella* (Battarbee et al. 2002; Winder et al. 2009). Most of the large-scale increases in *Cyclotella* species have been found in relatively pristine, nutrient poor and non-acidified lakes (Rühland et al. 2008). This increasing trend in planktic diatoms was directly associated with a decrease in benthic *Fragilaria* and (tycho)planktic *Aulacoseira* species. The longer ice-free period should overall be favourable to many diatom species, increasing overall competition within the lake, which would be unfavourable to *Fragilaria* species that typically thrive under longer periods of ice cover where competition within primary producer communities is limited (Lotter and Bigler 2000). The decrease in *Aulacoseira* species could be more directly

explained by the increased competition with the *Cyclotella* species, which are favoured by the changing lake conditions (Rühland and Smol 2005). Heavily silicified *Aulacoseira* species generally thrive under longer ice cover duration where there is less time for warming up the epilimnion, hence stronger mixing of the water column and no stratification. Inversely, the light *Cyclotella* species prefer shorter ice cover duration, allowing for higher epilimnion temperatures and stronger stratification of the water column (Rühland et al. 2015).

These trends have been observed in many lakes in the Northern Hemisphere, both in North America and Europe. However, possibly due to the shorter 25-year time span of this study, these longer time scale changes could not be observed. The absence of the trend could also be explained by the water chemistry of the lakes in this study. *Cyclotella* species have been shown to favour non-acidified lakes (Saros and Anderson 2015). In a study conducted by Rühland et al. (2003), observing 50 lakes in the Canadian Arctic, the pH of the 50 lakes were neutral to alkaline, which are ideal pH conditions for *Cyclotella* species. However, the 26 lakes in this study are dominantly slightly acidic, with pH values ranging from 5 to 7.5 (mean 6.4), which could partly explain their lack of presence in the recent samples. Additionally, these planktic species are favoured by greater water depth, which explains their presence in the Ba lakes. However, when these deeper Ba lakes are excluded, the average depth of the lakes in the dataset is 4.3m (ranging from 1.4m to 9.6m) which does not favour, although it does not completely preclude, planktic species.

Finally, while most of the observed changes in this study were attributed to changing climate and increasing temperatures, it is key to remember that lakes are complex ecosystems. Changes in diatom assemblages cannot be attributed to one single external factor. Nutrient loading, water stratification, erosion rate, water pH, biological population of the lake, habitat availability, prey-predator relationship, as well as numerous other factors all work together and behave differently in each and every lake.

6. Conclusions

The purpose of this thesis was to compare and analyse the impacts of evolving climate trends on diatom communities over a period of 25 years in Northwestern Finnish Lapland. While many palaeolimnological studies reconstruct ecosystems over long time frames, ranging from centuries to thousands of years, the present study aimed to observe changes in diatom communities over a short time scale. During the 25-year period between the original study by Weckström and Korhola (2001) and 2020, seasonal trends of climate warming were recorded in the region. These were defined by increases in yearly temperatures, but most strongly over the fall period between the months of September and October. Overall, a small majority of the 26 lakes studied have remained relatively stable with few to no changes to the diatom assemblages in the lake sediments. Only four of these lakes, scattered across the three vegetation zones, have sustained large changes at either the taxa or genus level. Most of the changes associated with these four lakes were related to major shifts in dominant diatom species. While some of these changes could be attributed to changing lake dynamics due to increasing temperatures and decreasing lake ice cover duration, they do not follow the global pattern observed in other literature. Many recent articles have observed an increase in dominance of *Cyclotella* species, directly associated to the decline of *Fragilaria* and *Aulacoseira* species. The shallow acidic nature of the lakes studied for this thesis could be the reason why this trend was not observed in the study lakes over the past 25 years. Another eight lakes were observed to have sustained moderate changes, where dominance changes were recorded for a few species while the majority remained unchanged. Of these eight lakes, half were from the SPB vegetation zone, which has experienced the most changes across the study area. This is likely due to more direct impacts of changing temperatures due to the lower altitude of the lakes. The remaining 14 lakes did not show noticeable changes in diatom communities and hence lake chemistry. In some cases, such as lakes in the Ba area, the lack of change could also be attributed to slow sedimentation rates, preventing the differentiation between old and newer samples. Repeating a similar study in another 25 years period (50 years after the original study) could enable validation of the current observations, shed new light regarding changes in the Ba lakes, and support determination of whether or not these lakes in Northwestern Finnish Lapland will experience the same changes as other northern hemisphere lakes under the continuing climate warming.

7. Acknowledgements

This adventure has been a crazy ride, from the change of topic due to the pandemic, to the writer's block after months of work on this project. It has been an extremely exciting experience, having the opportunity to meet and work with amazing people, and also visiting some of the most beautiful places I've had the chance to see. None of this would have been possible without my amazing supervisors. I would like to thank Jan Weckström for joining me during the field mission and for tolerating me and the countless diatom pictures I sent him asking for his help. I would like to thank Kaarina Weckström for rescuing me over a year ago when I was struggling to find a thesis topic, and also for the continuous support with the writing process. I am very grateful to Maija Heikkilä and the other members of the research group for the emotional and academic support with the very helpful "Monday morning coffees". Financial support from the Arctic Avenue is also gratefully acknowledged.

I would like to thank all of my friends and family for helping me get through this process. It is amazing to look back and see the incredible amount of support I have received over the past year. Thank you to my parents for putting up with me and my mood swings over this difficult process. I am very grateful to my friends in Finland that have not only helped me study but also helped me grow as a person. Thank you to all the people that took part in the Arctic field course for helping me collect some of the samples that were analysed in this thesis. Special thanks to the Järviryhmä group for the amazing time walking across the tundra while trying to teach me Finnish words. Thank you to Sanna and Kimmo for joining us last summer in Lapland for the field mission. There are so many other people that I could thank for their involvement in this adventure and I am sorry if I have not directly mentioned you here, but I hope that my actions have been able to show you my gratitude.

8. Citations

Aalto J, Karlsson P, Kaukoranta J-P, et al (2012) Tilastoja Suomen ilmastosta 1981-2010. Ilmatieteen laitos, Helsinki

Anderson NJ (2000) Miniview: diatoms, temperature and climatic change. European Journal of Phycology 35:307–314

Battarbee RW, Grytnes J-A, Thompson R, et al (2002) Comparing palaeolimnological and instrumental evidence of climate change for remote mountain lakes over the last 200 years. Journal of Paleolimnology 28:161–179

Bennett JR, Cumming BF, Ginn BK, Smol JP (2010) Broad-scale environmental response and niche conservatism in lacustrine diatom communities. Global Ecology and Biogeography 19:724–732

Benoiston A-S, Ibarbalz FM, Bittner L, et al (2017) The evolution of diatoms and their biogeochemical functions. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160397

Birks H (1998) DG Frey and ES Deevey Review 1: Numerical tools in palaeolimnology–Progress, potentialities, and problems. Journal of paleolimnology 20:307–332

Blom T, Korhola A, Weckström J (1998) Physical and chemical characterisation of small subarctic lakes in Finnish Lapland with special reference to climate change scenarios. pp 576–587

Cohen, A. S. (2003). Paleolimnology: the history and evolution of lake systems. Oxford University Press.

Filazzola A, Blagrave K, Imrit MA, Sharma S (2020) Climate change drives increases in extreme events for lake ice in the Northern Hemisphere. Geophysical Research Letters 47:e2020GL089608

Finnish Meteorological Institute. (2020). Monthly mean temperature observations: Enontekiö Kilpisjärvi Saana and Muonio kirkonkylä. Available: https://en.ilmatieteenlaitos.fi/download-observations

Frolova L, Nigmatullin N, Frolova A (2018) Paleolimnological studies of tundra lakes in the Pechora Delta (Nenets Autonomous Region, Russia). International Multidisciplinary Scientific GeoConference: SGEM 18:621–627

Gadagkar R (1989) An undersirable property of Hill's diversity index N2. Oecologia 80:140–141

Garamvoelgyi A, Hufnagel L (2013) Impacts of climate change on vegetation distribution no. 1 climate change induced vegetation shifts in the palearctic region. Applied Ecology and Environmental Research 11:79–122

Gebre S, Boissy T, Alfredsen K (2014) Sensitivity of lake ice regimes to climate change in the Nordic region. The Cryosphere 8:1589–1605

González Ortiz, A., Guerreiro, C., & Soares, J. (2020). Air quality in Europe: 2020 report. Publications Office of the European Union.

Hämet-Ahti L, Ruuhijärvi R, Suominen J (1988) Vegetation and flora. In: Alalammi P (ed) Atlas of Finland. National Board of Survey, Geographical Society of Finland, Helsinki

Hartley B, Ross R, Williams DM (1986) A check-list of the freshwater, brackish and marine diatoms of the British Isles and adjoining coastal waters. Journal of the Marine Biological Association of the United Kingdom Plymouth 66:531–610

Hausfather Z, Drake HF, Abbott T, Schmidt GA (2020) Evaluating the performance of past climate model projections. Geophysical Research Letters 47:e2019GL085378

Havens K, Jeppesen E (2018) Ecological responses of lakes to climate change. Water 10:917.

Hettelingh J-P, Downing RJ, de Smet PA (1992) The critical loads concept for the control of acidification. In: Studies in Environmental Science. Elsevier, pp 161–174

IPCC, 2018: Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [V. Masson-Delmotte, P. Zhai, et al. (eds.)]. In Press.

Johansson K (1985) Mercury in sediment in Swedish forest lakes: With 2 figures in the text. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen 22:2359–2363

Juggins. S. 2007 C2 Version 1.5 User guide. Software for ecological and palaeoecological data analysis and visualisation. Newcastle University, Newcastle upon Tyne, UK. 73pp.

Krammer, K. & H. Lange-Bertalot, 1986. Bacillariophyceae. 1. Teil: Naviculaceae. In Ettl, H., J. Gerloff, H. Heynig & D. Mollenhauer (eds), Süsswasser flora von Mitteleuropa, Band 2/1. Gustav Fischer Verlag: Stuttgart.

Krammer, K. & H. Lange-Bertalot, 1988. Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. In Ettl, H., J. Gerloff, H. Heynig & D. Mollenhauer (eds), Süsswasserflora von Mitteleuropa, Band 2/2. VEB Gustav Fischer Verlag: Stuttgart.

Krammer, K. & H. Lange-Bertalot, 1991a. Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. In Ettl, H., J. Gerloff, H. Heynig & D. Mollenhauer (eds), Süsswasserflora von Mitteleuropa, Band 2/3. Gustav Fischer Verlag: Stuttgart.

Krammer, K. & H. Lange-Bertalot, 1991b. Bacillariophyceae. 4. Teil: Achnanthaceae, Kritische Ergänzungen zu *Navicula* (Lineolatae) und *Gomphonema*, Gesamtliteraturverzeichnis Teil 1–4. In Ettl, H., J. Gerloff, H. Heynig & D. Mollenhauer (eds), Süsswasserflora von Mitteleuropa, Band 2/4. Gustav Fischer Verlag: Stuttgart.

Kennedy J, Morice C, Parker D, Kendon M (2016) Global and regional climate in 2015. Weather 71:185–192

Korhola A (1999) Distribution patterns of Cladocera in subarctic Fennoscandian lakes and their potential in environmental reconstruction. Ecography 22:357–373

Korhola A, Weckström J (2004) Paleolimnological studies in arctic Fennoscandia and the Kola Peninsula (Russia). In: Long-term environmental change in Arctic and Antarctic lakes. Springer, pp 381–418

Korhonen J (2019) Long-term changes and variability of the winter and spring season hydrological regime in Finland (Doctoral dissertation). The University of Helsinki.

Lotter AF, Bigler C (2000) Do diatoms in the Swiss Alps reflect the length of ice cover? Aquatic sciences 62:125–141

Mann ME, Rahmstorf S, Steinman BA, et al (2016) The likelihood of recent record warmth. Scientific reports 6:1–7

Merkouriadi I, Leppäranta M, Järvinen O (2017) Interannual variability and trends in winter weather and snow conditions in Finnish Lapland. Estonian Journal of Earth Sciences 66:47-57

Moser K, MacDonald G, Smol J (1996) Applications of freshwater diatoms to geographical research. Progress in Physical Geography 20:21–52

Patrick R, Reimer CW (1966) The Diatoms of the United States, Exclusive of Alaska and Hawaii: Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaca. Academy of Natural Sciences of Philadelphia, Philadelphia

Pienitz R, Smol JP, Birks HJB (1995) Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. Journal of Paleolimnology 13:21–49

Rautio M, Sorvari S, Korhola A (2000) Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajärvi. Journal of Limnology 59:81–96

Reeves, C. C. (2014). Introduction to paleolimnology. Elsevier.

Rekolainen S, Verta M, Liehu A (1986) The effect of airborne mercury and peatland drainage on sediment mercury contents in some Finnish forest lakes. Publications of the water research institute. Vesihallitus – National Board of Waters, Finland, Helsinki

Renberg I, Hansson H (2008) The HTH sediment corer. Journal of Paleolimnology 40:655–659

Reynolds CS (1984) The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge

Round FE, Crawford RM, Mann DG (1990) The diatoms : biology & morphology of the genera, Reprinted 1992, 1996, 2000. Cambridge University Press, Cambridge

Rühland K, Paterson AM, Smol JP (2008) Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Global Change Biology 14:2740–2754

Rühland K, Priesnitz A, Smol JP (2003) Paleolimnological evidence from diatoms for recent environmental changes in 50 lakes across Canadian Arctic treeline. Arctic, Antarctic, and Alpine Research 35:110–123

Rühland K, Smol JP (2005) Diatom shifts as evidence for recent Subarctic warming in a remote tundra lake, NWT, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 226:1–16

Rühland KM, Paterson AM, Smol JP (2015) Lake diatom responses to warming: reviewing the evidence. Journal of paleolimnology 54:1–35

Saros J, Anderson N (2015) The ecology of the planktonic diatom Cyclotella and its implications for global environmental change studies. Biological Reviews 90:522–541

Sharma S, Blagrave K, Magnuson JJ, et al (2019) Widespread loss of lake ice around the Northern Hemisphere in a warming world. Nature Climate Change 9:227–231

Simonen Ahti (1980) The Precambrian in Finland. Geologinen tutkimuslaitos, Espoo

Smol JP (2009) Pollution of Lakes and Rivers: A Paleoenvironmental Perspective, 2. Aufl. Wiley-Blackwell, Hoboken

Stoermer EF, Smol JP (1999) The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, Cambridge

SWIPA (2017) Snow, Water, Ice and Permafrost in the Arctic. Arctic Monitoring and Assessment Programme, Oslo, Norway

ter Braak CJ (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179

ter Braak CJ, Šmilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: Software 675 for Ordination (version 5.0). Microcomputer power, Itaca

Tikkanen M (2002) Long-term changes in lake and river systems in Finland. Fennia-International Journal of Geography 180:31–42

Vincent WF, Laurion I, Pienitz R, Walter Anthony K (2013) Climate impacts on Arctic lake ecosystems. Climatic change and global warming of inland waters: Impacts and mitigation for ecosystems and societies 27-28.

Weckström J, Korhola A (2001) Patterns in the distribution, composition and diversity of diatom assemblages in relation to ecoclimatic factors in Arctic Lapland. Journal of Biogeography 28:31–45

Weckström J, Korhola A, Blom T (1997a) The relationship between diatoms and water temperature in thirty subarctic Fennoscandian lakes. Arctic and Alpine Research 29:75–92

Weckström J, Korhola A, Blom T (1997b) Diatoms as quantitative indicators of pH and water temperature in subarctic Fennoscandian lakes. Hydrobiologia 347:171–184

Werner D (1977) The Biology of Diatoms. University of California Press, Berkeley and Los Angeles

World Health Organization. (2018). Global Air Quality Database App: App for exploring air quality in countries. *WHO Global Air Quality Database* (update 2018) edition. Version 1.0. Geneva.

Winder M, Reuter JE, Schladow SG (2009) Lake warming favours small-sized planktonic diatom species. Proceedings of the Royal Society B: Biological Sciences 276:427–435

Wolfel AP, Kling HJ (2001) A consideration of some North American soft-water Brachysira taxa and description ofB. arctoborealis sp. nov. Studies on Diatoms (R Jahn, JP Kociolek, A Witkowski, P Compàre & H Lange-Bertalot) Koeltz, Koenigstein 243–264

Woolway RI, Merchant CJ (2019) Worldwide alteration of lake mixing regimes in response to climate change. Nature Geoscience 12:271–276

9. Appendix

Appendix 1: Abbreviations of diatom species used in the DCA and CCA analyses.

Taxa	Abbreviation
Achnanthes levanderi	*Ac. levanderi*
Achnanthes marginulata	*Ac. margi.*
Achnanthes pusilla	*Ac. pusilla*
Aulacoseira distans var. *alpigena*	*Au. distans alpi.*
Aulacoseira distans var. *distans*	*Au. distans*
Aulacoseira distans var. *nivalis*	*Au. distans. niv.*
Aulacoseira lirata var. *lirata*	*Au. lirata*
Aulacoseira perglabra	*Au. pergla.*
Brachysira brebissonii	*Bra. brebi.*
Brachysira vitrea	*Bra. vitrea*
Cyclotella comensis	*Cy. comensis*
Cyclotella glomerata	*Cy. glomerata*
Cyclotella rossii	*Cy. rossii*
Cymbella gaeumannii	*Cym. gaeum.*
Eunotia rhomboidea	*Eu. rhombo.*
Fragilaria brevistriata var. *brevistriata*	*Fr. brevi.*
Fragilaria construens var. *exigua*	*Fr. cons. exi.*
Fragilaria construens var. *venter*	*Fr. cons. ven.*
Fragilaria pinnata var. *pinnata*	*Fr. pinnata*
Fragilaria pseudoconstruens	*Fr. pseudo.*
Frustulia rhomboides var. *rhomboides*	*Fru. rhom.*
Frustulia rhomboides var. *saxonica*	*Fru. rh. sa.*
Navicula hoeflerii	*Nav. hoefl.*
Navicula pupula	*Nav. pup.*
Navicula radiosa var. *radiosa*	*Nav. radiosa*
Navicula subtilissima	*Nav. subti.*
Pinnularia biceps var. *biceps*	*Pin. biceps*
Pinnularia rupestris	*Pin. rupes.*

Appendix 2 Locations and environmental characteristic of the study lakes.

Lake	Latitude	Longitude	Altitude	Area	Mire area	SPB	MBW	Ba	Max.depth	AirT	pH	Cond.	Alkalinity	LOI***	TOC	Na	K	Mg
WFL3	67.85	24.18	268.00	7.14	40.03	1.00	0.00	0.00	4.00	13.30	6.10	10.69	2.44	64.10	9.90	0.65	0.17	0.27
WFL4	67.98	23.68	262.00	10.67	28.81	1.00	0.00	0.00	3.30	13.10	4.80	7.20	0.00	71.80	8.30	0.43	0.11	0.14
WFL5	68.01	23.40	249.00	4.34	45.95	1.00	0.00	0.00	3.35	13.20	5.90	18.70	9.76	50.10	11.00	1.20	0.17	0.71
WFL6	68.12	23.37	252.00	1.52	4.45	1.00	0.00	0.00	4.30	13.10	6.20	6.40	1.22	88.00	5.10	0.15	0.11	0.03
WFL7	68.20	23.18	263.00	0.90	0.00	1.00	0.00	0.00	4.40	12.60	6.50	16.00	4.50	61.20	7.20	0.80	0.22	0.36
WFL11	68.40	22.85	313.00	2.18	2.38	1.00	0.00	0.00	4.10	12.60	6.60	9.40	4.27	58.60	8.00	0.73	0.32	0.27
WFL12	68.42	22.58	332.00	1.97	58.82	1.00	0.00	0.00	1.85	12.40	4.40	13.50	0.61	80.80	11.60	1.32	0.20	0.20
WFL13	68.47	22.43	322.00	2.55	25.75	1.00	0.00	0.00	4.00	12.50	6.30	11.90	4.27	60.40	8.50	0.60	0.34	0.41
WFL17	68.90	21.07	463.00	6.05	0.93	0.00	1.00	0.00	1.70	11.30	6.90	23.90	6.10	48.30	10.40	1.56	0.59	0.56
WFL18	68.92	20.97	526.00	3.85	0.00	0.00	1.00	0.00	1.45	10.80	7.20	37.70	8.50	55.00	8.90	1.39	0.82	0.54
WFL24	69.05	20.87	679.40	69.86	0.00	0.00	0.00	1.00	24.00	9.90	6.80	27.70	0.16	20.50	3.10	1.15	0.27	0.67
WFL25	69.07	20.88	941.00	1.69	0.00	0.00	0.00	1.00	3.35	8.50	6.20	7.20	2.00	4.69	3.50	0.33	0.38	0.08
WFL26	69.18	20.72	360.00	7.21	0.00	0.00	1.00	0.00	3.40	11.10	6.90	34.20	6.50	22.67	9.80	1.69	2.29	0.43
WFL27	69.08	20.80	593.00	15.68	0.00	0.00	0.00	1.00	13.75	10.40	7.10	24.00	5.50	18.42	4.10	0.86	1.69	0.22
WFL29	68.10	23.42	249.00	4.01	12.03	1.00	0.00	0.00	9.60	13.20	6.00	17.20	6.10	42.30	12.40	0.90	0.18	0.49
WFL30	68.13	23.37	253.00	1.33	0.00	1.00	0.00	0.00	4.30	13.20	4.00	5.20	0.61	83.60	11.30	0.22	0.08	0.08
WFL32	68.42	22.90	319.00	28.18	22.68	1.00	0.00	0.00	6.00	12.60	7.00	29.30	10.98	42.30	8.30	1.34	0.57	0.90
WFL35	68.68	22.05	526.00	13.91	0.00	0.00	1.00	0.00	5.35	11.00	7.40	28.00	9.00	38.20	4.90	0.80	0.35	0.40
WFL36	68.67	22.05	498.00	10.27	0.33	0.00	1.00	0.00	17.00	11.30	7.50	33.50	9.50	35.70	6.50	0.98	0.40	0.48
WFL37	68.67	22.03	508.00	1.39	0.00	0.00	1.00	0.00	2.85	11.20	7.30	32.80	9.50	38.20	4.80	1.01	0.47	0.38
WFL41	68.92	21.05	596.00	3.47	0.00	0.00	1.00	0.00	8.15	10.50	6.80	13.30	3.66	54.50	4.00	0.95	0.43	0.27
WFL49	69.08	20.67	778.00	16.10	0.00	0.00	0.00	1.00	12.10	9.40	7.00	9.90	8.00	16.90	2.50	0.58	0.16	0.11
WFL52	69.05	20.98	687.00	16.89	0.00	0.00	0.00	1.00	9.10	9.90	6.60	18.20	0.11	19.60	4.40	1.14	0.35	0.41
WFL54	69.03	21.13	796.40	9.33	0.00	0.00	0.00	1.00	8.00	9.20	7.00	12.80	3.66	33.61	3.00	0.84	0.28	0.19
WFL55	69.06	21.05	774.00	20.44	0.00	0.00	0.00	1.00	2.00	9.30	7.00	11.60	4.27	34.04	2.50	0.53	0.24	0.20
WFL56	69.17	21.05	1009.00	9.61	0.00	0.00	0.00	1.00	10.00	7.90	5.60	5.90	0.00	13.49	1.50	0.44	0.09	0.06

Appendix 3: Species name and associated code of every diatom specie observed and examined in this thesis. The row # Occurrence represents the amount of lakes in which diatom species were observed. The row Max % represents the maximum occurrence of the selected specie within the lakes in which it appeared. Hill's N2 represents the effective number of occurrences of the selected specie within the data.

Taxon code	**Taxa**	**Author**	**# Occurrence**	**Hill's N2** (Gadagkar 1989)	**Max %**
AC018A	*Achnanthes laterostrata*	Hust (1933)	4	3.58	0.38
AC022A	*Achnanthes marginulata*	Grun. in Cleve & Grun (1880)	4	1.51	15.59
AC046A	*Achnanthes altaica*	A. Cleve-Euler (1953)	6	4.54	1.30
AC152A	*Achnanthes carissima*	Lange-Bertalot (1990)	1	1.00	6.30
AC023A	*Achnanthes conspicua* var. *conspicua*	A. Mayer (1919)	1	1.00	0.18
FSN004	*Achnanthes daonensis*	NORD-CHILL (1997)	9	5.17	1.79
AC024A	*Achnanthes depressa*	Hust (1933)	6	3.59	0.83
AC039A	*Achnanthes didyma*	Hust (1933)	1	1.00	0.17
AC025A	*Achnanthes flexella*	Brun (1880)	4	3.21	0.58
AC154A	*Achnanthes imperfecta*	Schimanski (1978)	5	4.51	0.35
AC083A	*Achnanthes laevis*	Ostr (1910)	1	1.00	0.17
AC044A	*Achnanthes levanderi*	Hust (1933)	23	8.54	20.67
FSN001	*Achnanthes minutissima*	NORD-CHILL (1997)	18	9.32	9.91
AC019A	*Achnanthes nodosa*	A. Cleve-Euler (1900)	17	11.01	3.01
AC035B	*Achnanthes petersenii*	Hust (1936)	3	1.80	1.47
AC035A	*Achnanthes pusilla*	Grun. in Cleve & Grun (1880)	16	5.63	14.23
AC034A	*Achnanthes suchlandtii*	Hust (1933)	5	3.24	1.23
AC042A	*Achnanthes subatomoides*	Lange-Bertalot & Archibald (1985)	13	8.32	3.02
AC160A	*Achnanthes thermalis*	Rabenhorst (1907)	3	2.15	3.48
AC161A	*Achnanthes sublaevis*	Hust (1936)	3	2.81	0.38
AT001A	*Actinella punctata*	Lewis	2	1.49	0.76
AM011A	*Amphora libyca*	Her	2	1.38	0.90

AM001A	*Amphora ovalis*	Kutz (1844)	1	1.00	0.19
AU004D	*Aulacoseira distans* var. *alpigena*	Simonsen (1979)	1	1.00	11.30
AU001D	*Aulacoseira italica f. crenulata*	R. Ross in Hartley (1986)	2	1.26	3.78
AU005A	*Aulacoseira distans* var. *distans*	Simonsen (1979)	18	9.20	19.70
AU005E	*Aulacoseira distans* var. *nivalis*		6	4.19	2.90
AU004B	*Aulacoseira lirata* var. *lacustris*	R. Ross in Hartley (1986)	3	2.81	2.25
AU004A	*Aulacoseira lirata* var. *lirata*	R. Ross in Hartley (1986)	6	4.48	4.73
AU014A	*Aulacoseira nygaardii*	Camburn	1	1.00	0.66
AU010A	*Aulacoseira perglabra*		5	3.22	10.54
FSN013	*Aulacoseira subarctica*	NORD-CHILL (1997)	3	1.97	14.63
AU001C	*Aulacoseira italica var. valida*	Simonsen (1979)	10	6.91	3.82
BR006A	*Brachysira brebissonii*	R. Ross in Hartley (1986)	20	11.19	13.91
BR002A	*Brachysira follis*	R. Ross in Hartley (1986)	1	1.00	0.17
BR003A	*Brachysira serians*	Round & Mann (1981)	4	2.10	3.15
BR004A	*Brachysira styriaca*	R. Ross in Hartley (1986)	1	1.00	0.16
BR001A	*Brachysira vitrea*	R. Ross in Hartley (1986)	20	8.20	16.18
BR005A	*Brachysira zellensis*	Round & Mann (1981)	1	1.00	1.47
CA002A	*Caloneis bacillum*	Cleve (1894)	1	1.00	0.56
CA031A	*Caloneis obtusa*	Cleve (1894)	1	1.00	0.18
CA018A	*Caloneis tenuis*	Gregory (1985)	2	1.32	1.10
CP002B	*Campylodiscus noricus* var. *hibernicus*	Grun (1862)	1	1.00	0.18
CO001A	*Cocconeis placentula var. placentula*	Ehrenb (1838)	2	1.83	0.35
CY013A	*Cyclotella antigua*	W. Sm (1853)	2	1.41	0.92
FSN020	*Cyclotella bodanica* var. *lemanica*	NORD-CHILL (1997)	4	1.80	4.06
CY010A	*Cyclotella comensis*	Grun. in Van Heurck (1882)	2	1.03	13.40

CY052A	*Cyclotella rossii*	Hakansson (1990)	6	2.13	26.10
CY055A	*Cyclotella schumannii*	Hakansson (1990)	2	1.19	3.53
CY004A	*Cyclotella stelligera*	Grun. in Van Heurck (1882)	1	1.00	4.49
CL001A	*Cymatopleura solea*	W. Smith (1851)	1	1.00	0.19
ABC001	*Cymbella alpina*		1	1.00	0.39
CM016A	*Cymbella amphicephala*	Naegeli ex Kutz (1849)	1	1.00	0.39
CM015A	*Cymbella cesatii*	Grun. in A. Schmidt (1881)	8	5.36	5.60
CM026A	*Cymbella cuspidata*	Kutz (1844)	1	1.00	0.20
CM038A	*Cymbella delicatula*	Kutz (1849)	1	1.00	0.18
CM052A	*Cymbella descripta*	Krammer & Lange-Bertalot (1985)	9	5.15	3.90
EY006A	*Cymbella elginensis*	Krammer (1981)	1	1.00	0.36
CM020A	*Cymbella gaeumannii*	Meister (1934)	2	1.53	1.66
CM048A	*Cymbella lunata*	W. Sm. in Grev. (1855)	10	7.16	1.58
EY003A	*Cymbella hebridica*	Cleve (1894)	4	1.96	3.83
CM013A	*Cymbella helvetica* var. *helvetica*	Kutz (1844)	1	1.00	0.19
CM101B	*Cymbella incerta*	Grun. in Cleve & Moller (1878)	7	4.29	2.34
CM004A	*Cymbella microcephala*	Grun. in Van Heurck (1880)	5	3.58	1.10
EY011A	*Cymbella minuta*	Hilse ex Rabenh (1862)	3	2.08	1.42
CM009A	*Cymbella naviculiformis*	Auersw. ex Heib (1863)	13	5.72	9.61
EY013A	*Cymbella obscura*	Krasske (1938)	8	5.21	2.72
EY014A	*Cymbella perpusilla*	A. Cleve (1895)	13	6.75	3.16
ABC002	*Cymbella proxima*		4	3.62	0.35
ABC003	*Cymbella pusilla*		1	1.00	0.39
EY016A	*Cymbella silesiaca*	Bleisch ex Rabenh (1864)	24	13.72	4.71
RE001A	*Cymbella sinuata*	Greg (1856)	2	1.81	0.37
CM107A	*Cymbella subcuspidata*	Krammer (1982)	1	1.00	0.37
DE003A	*Denticula kuetzingii*	Grun	1	1.00	2.73
FSN028	*Denticula tenuis*	NORD-CHILL (1997)	4	3.38	3.01
DP012A	*Diploneis marginestriata*	Hust (1922)	2	1.59	0.58
EU013A	*Eunotia arcus*	Ehrenb (1837)	1	1.00	0.18

EU014A	*Eunotia bactriana*	Ehrenb (1854)	2	1.22	3.58
EU049A	*Eunotia curvata*	Lagerst (1884)	12	5.37	6.60
EU049B	*Eunotia curvata* var. *subarcuata*	Woodhead & Tweed (1954)	2	1.62	0.57
EU015A	*Eunotia denticulata*	Rabenh (1864)	2	2.00	0.58
EU016A	*Eunotia diodon*	Ehrenb (1837)	4	2.12	1.39
EU043A	*Eunotia elegans*	Ostr (1910)	1	1.00	0.17
EU009A	*Eunotia exigua*	Rabenh (1864)	13	3.58	6.23
EU051A	*Eunotia vanheurckii*	Patr (1958)	9	2.81	6.79
EU017A	*Eunotia flexuosa*	Kutz (1849)	3	1.90	1.26
EU024A	*Eunotia glacialis*	Meister (1912)	9	6.63	1.18
EU054A	*Eunotia hexaglyphis*	Ehrenb (1854)	1	1.00	0.17
EU002E	*Eunotia pectinalis* var. *minor f. impressa*	Hust	2	2.00	0.18
EU047A	*Eunotia incisa*	W. Sm. ex Greg (1854)	10	7.96	0.70
EU048A	*Eunotia naegelii*	Migula (1907)	1	1.00	0.33
EU045A	*Eunotia nymanniana*	Grun. in Van Heurck (1881)	3	2.20	1.28
EU034A	*Eunotia parallela* var. *parallela*	Ehrenb (1843)	1	1.00	0.36
EU002D	*Eunotia pectinalis* var. *undulata*	Rabenh (1864)	2	2.00	0.18
EU003A	*Eunotia praerupta*	Ehrenb. (1843)	15	9.31	2.60
FSN034	*Eunotia praerupta* var. *bigibba*	NORD-CHILL (1997)	1	1.00	0.19
EU011A	*Eunotia rhomboidea*	Hust (1950)	11	4.99	4.34
EU106A	*Eunotia rhynchocephala*	Hustedt (1936)	1	1.00	0.33
EU032A	*Eunotia serra*	Ehrenb (1837)	7	5.54	1.16
ABC005	*Eunotia soleirolii*		2	1.62	0.53
ABC006	*Eunotia subarcuatoides*		1	1.00	0.54
EU039A	*Eunotia triodon*	Ehrenb (1837)	2	1.98	0.93
PS001A	*Fragilaria brevistriata var. brevistriata*	Grun. in Van Heurck (1885)	12	5.82	3.77
FR009A	*Fragilaria capucina* var. *capucina*	Desm (1825)	2	1.84	0.97
FF003A	*Fragilaria constricta* f. *constricta*	Ehrenb (1843)	4	3.22	0.52
FR010B	*Fragilaria constricta* f. *stricta*	Hust (1931)	1	1.00	3.30
SR001A	*Fragilaria construens* var. *construens*	Grun (1862)	3	1.76	4.17
FR002B	*Fragilaria construens* var. *binodis*	Grun (1862)	2	2.00	0.19

FR002D	*Fragilaria construens* var. *exigua*		13	6.87	13.69
FR002C	*Fragilaria construens* var. *venter*	Grun. in Van Heurck (1881)	5	2.75	36.07
SS001A	*Fragilaria lapponica*	Grun. in Van Heurck (1881)	3	1.91	1.51
SS002A	*Fragilaria pinnata* var. *pinnata*	Ehrenb (1843)	11	7.04	4.54
PS002A	*Fragilaria pseudoconstruens*	Marciniak (1982)	9	5.97	9.06
SF001A	*Fragilaria virescens* var. *exigua*	Grun. in Van Heurck (1881)	7	5.13	6.09
FU002A	*Frustulia rhomboides* var. *rhomboides*	De Toni (1891)	23	11.38	23.73
FU002B	*Frustulia rhomboides* var. *saxonica*	De Toni (1891)	18	10.54	24.79
FU002F	*Frustulia rhomboides* var. *viridula*	Cleve (1894)	7	4.04	4.95
GO006A	*Gomphonema acuminatum* var. *acuminatum*	Ehrenb (1832)	9	7.37	0.83
GO029A	*Gomphonema* cf. *clavatum*	Her	1	1.00	0.55
GO004A	*Gomphonema gracile*	Ehrenb (1838)	2	1.48	0.72
GO013A	*Gomphonema parvulum* var. *parvulum*	Kutz (1849)	15	7.85	3.60
ABC007	*Gomphonema pseudoaugur*		1	1.00	0.35
ABC008	*Gyrosigma attenuatum*		1	1.00	0.19
MR001A	*Meridion circulare* var. *circulare*	Ag (1831)	1	1.00	0.20
MR001B	*Meridion circulare* var. *constrictum*	Van Heurck (1885)	1	1.00	0.17
NA161A	*Navicula absoluta*	Hust (1950)	6	3.83	2.30
NA069A	*Navicula americana*	Ehrenb (1843)	2	2.00	0.39
NA038A	*Navicula arvensis*	Hust	1	1.00	0.59
CV001A	*Navicula cocconeiformis* var. *cocconeiformis*	Greg. ex Greville (1855)	5	2.43	1.74
NA007A	*Navicula cryptocephala* var. *cryptocephala*	Kutz (1844)	6	3.47	1.89
NA149A	*Navicula digitulus*	Hust (1943)	3	2.32	1.54
NA100A	*Navicula explanata*	Hust (1948)	2	1.82	0.36
NA015A	*Navicula hassiaca*	Krasske (1925)	1	1.00	1.10
NA433C	*Navicula ignota* var. *palustris*	J.W.G. Lund (1946)	1	1.00	0.19

NA101A	*Navicula jaagii*	Meister (1934)	7	5.26	1.65
CV002A	*Navicula jaernefeltii*	Hust (1942)	2	1.99	0.19
FSN047	*Navicula pupula*	NORD-CHILL (1997)	15	3.37	16.64
NA156A	*Navicula leptostriata*	Jorgensen (1948)	8	4.74	5.60
NA006A	*Navicula mediocris*	Krasske (1932)	13	7.99	4.47
SL003A	*Navicula minima* var. *minima*	Grun. in Van Heurck (1880)	5	1.52	6.48
ABC009	*Navicula muraliformis*		1	1.00	0.93
CV004A	*Navicula pseudoscutiformis*	Hust (1930)	4	2.91	0.76
NA123A	*Navicula pseudoventralis*	Hust (1953)	1	1.00	0.19
NA003A	*Navicula radiosa* var. *radiosa*	Kutz (1844)	19	6.91	10.00
NA133A	*Navicula schassmannii*	Hust (1937)	10	4.02	3.68
SL002A	*Navicula seminulum*	Grun (1860)	17	9.10	7.03
NA048A	*Navicula soehrensis* var. *soehrensis*	Krasske (1923)	2	1.83	0.33
NA033A	*Navicula subtilissima*	Cleve (1891)	22	8.78	10.98
NA040A	*Navicula hoeflerii*	Choln. in Choln. & Schindler (1953)	12	4.10	30.00
NA738A	*Navicula vitiosa*	Schimanski (1978)	6	3.30	2.27
NE003A	*Neidium affine* var. *affine*	Pfitz (1871)	1	1.00	0.19
NE001C	*Neidium iridis* var. *ampliatum*	Cleve (1894)	4	2.30	2.88
NE004A	*Neidium bisulcatum* var. *bisulcatum*	Cleve (1894)	2	1.81	0.38
NE007A	*Neidium dubium* var. *dubium*	Cleve (1894)	6	3.19	3.18
NE001A	*Neidium iridis*	Cleve (1894)	10	5.53	2.75
NE9999	*Neidium* spp.		6	5.28	0.80
NI020A	*Nitzschia angustata* var. *angustata*	Grun. in Cleve & Grun (1880)	8	4.85	2.30
NI002A	*Nitzschia fonticola*	Grun. in Van Heurck (1881)	19	8.09	7.41
PI055A	*Pinnularia balfouriana*	Grun. ex Cleve (1896)	2	1.74	0.40
PI018A	*Pinnularia biceps* var. *biceps*	Greg (1856)	20	7.21	17.38
PI170A	*Pinnularia braunii*	Cleve	1	1.00	2.36

PI015A	*Pinnularia abaujensis*	R. Ross in Hartley (1986)	7	4.45	1.23
Pi015C	*Pinnularia abaujensis* var. *linearis*	Patr. in Patr. & Reimer (1966)	5	3.79	1.75
FSN056	*Pinnularia interrupta* var. *gibberula*	NORD-CHILL (1997)	6	4.45	1.05
FSN057	*Pinnularia microstauron*	NORD-CHILL (1997)	15	9.38	3.16
ABC010	*Pinnularia microstauron* var. *brebissoni*		3	2.34	0.71
FSN058	*Pinnularia nodosa*	NORD-CHILL (1997)	3	2.72	0.75
ABC011	*Pinnularia obscura*		1	1.00	1.22
FSN084	*Pinnularia pluviana*	Sovereign	1	1.00	0.20
PI056A	*Pinnularia rupestris*	Hantzsch in Rabenh (1861)	12	5.77	13.35
PI022A	*Pinnularia subcapitata* var. *subcapitata*	Greg (1856)	1	1.00	0.17
PI007A	*Pinnularia viridis* var. *viridis*	Ehrenb (1843)	14	8.44	2.46
RH001A	*Rhopalodia gibba* var. *gibba*	O. Mull (1895)	2	1.45	0.73
SA001A	*Stauroneis anceps* var. *anceps*	Ehrenb (1843)	15	9.14	5.19
SA006A	*Stauroneis phoenicenteron* var. *phoenicenteron*	Ehrenb (1843)	10	6.79	2.04
SP002A	*Stenopterobia sigmatella*	R. Ross in Hartley (1986)	3	2.77	1.11
ABC012	*Stephanodiscus hantzschii*		1	1.00	0.18
OX001A	*Tabellaria binalis*	Grun. in Van Heurck (1881)	2	1.86	2.16
OX001B	*Tabellaria binalis* var. *elliptica*	Flower (unpub) (1986)	1	1.00	0.20
FSN061	*Tabellaria flocculosa*	NORD-CHILL (1997)	23	13.89	5.69
TA004A	*Tabellaria quadriseptata*	Knudson (1952)	2	1.55	0.58
ABC013	*Tetracyclus emarginatus*		1	1.00	0.88
TE001A	*Tetracyclus lacustris*	Ralfs (1853)	8	5.27	1.58
CY007A	*Cyclotella glomerata*	Bachm (1911)	1	1.00	7.94
SE001A	*Semiorbis hemicyclus*	Patr. in Patr. & Reimer (1966)	2	1.33	2.04